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1937

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MARCH, 1938

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The present volume contains the contributions from the Woods Hole Oceanographic Institution which appeared during 1937 in publications other than *Papers in Physical Oceanography and Meteorology;* also the Annual Report of the Director.

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Report for the year 1936

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THE OCCURRENCE OF SAPROPHYTIC FUNGI IN MARINE MUDS

F. K. SPARROW, JR.

(From the Woods Hole Oceanographic Institution[1] and the Botany Department of the University of Michigan[2])

Introduction

Since it has been recognized for many years that fungi play an important and significant rôle in the disintegration of organic materials in land soils, it is natural to suspect that they might perform a similar function in sea bottoms. Previous papers (Petersen, 1905; Sparrow, 1934, 1936) have shown that in the littoral of certain localities in northern Europe and eastern United States there are true marine fungi which are active in initiating the destruction of living, autophytic marine plants and in certain cases also in aiding in their disintegration. As no systematic study of off-shore localities for the presence of wholly saprophytic fungi in the muds had been reported, the preliminary investigation described in this paper was undertaken during July–August, 1936, at the Woods Hole Oceanographic Institution.

Stations

The following are the locations of stations selected for study and from which the mud cores were obtained. All were in localities marked " sticky " or " sand and mud " on the hydrographic charts.

Station 1. One-half mile N.W. of Weepecket Rock Buoy, Buzzard's Bay. *Depth:* 18.0 meters.

Station 2. Western entrance to Vineyard Sound, 3¼ miles E. of Vineyard Sound Whistling Buoy, 5¼ miles W. by S., ¾ S. on Gay Head Light. *Depth:* 32.7 meters.

Station 3. Gulf of Maine, 45°35′ N., 69°11′ W. (Atlantis Station No. 2640). *Depth:* 163.6 meters.

Station 4. Gulf of Maine, 42°19′ N., 69°20′ W. *Depth:* 220 meters.

Portions of two cores collected by Dr. Henry Stetson from the Gulf of Maine and labelled " Canyon B " (depth 1127.2 meters; Station No. 5, Table I) and " Canyon E " (depth 718.0 meters; Station No. 6, Table

[1] Contribution No. 73.
[2] Contribution No. 630.

I) were obtained from Dr. S. A. Waksman. Since these had previously been partly used for bacteriological purposes and had been stored for some days they were considered questionable sources of data.

Methods and Results

In order to obtain any significant information in the limited time available, the methods outlined below were considered most practical even though they were subject to very definite limitations.

Collection of Cores

The apparatus commonly used in the collection of stratified mud cores for bacteriological purposes was employed. This is a modification of the instrument used by Moore and Neil (1930) in the Clyde Sea area. To eliminate as far as possible contamination during collection, all parts of the sampling apparatus in contact with the sterilized glass tube were thoroughly swabbed with 10 per cent formalin immediately before use. However, trials with swabbed and unswabbed apparatus showed little difference in the number of colonies of fungi obtained. All the usual precautions were employed to keep the cores free from contamination after collection. The lengths of the cores varied but averaged about 12 cm.; their diameter was 18 mm.

Recovery of Fungi

After the tubes containing the cores were brought into the laboratory, the upper cork was flamed, the free water removed, and the supernatant liquid immediately above the mud put in a sterile container for future use. The core was then "blown" under sterile conditions into a sterilized Petri dish and the outside surface and ends removed with a hot scalpel as an additional precaution against contamination during collection.

Two methods were followed in recovering the fungi. The first, practised extensively in the study of fresh-water fungi, involves the use of water cultures. Five jars of sterilized sea water were prepared into each of which was placed a core from Station 2, a site at which cores were readily obtainable. The cores were broken up in the water, the mixture allowed to settle, and 20–30 dead *Calanus finmarchicus* and *Saggita* from Station 2 were added. Three jars were kept at room temperature (23° C.) in the light and two in the dark at about 6° C. Bits of "shiner" (a small marine fish) removed aseptically were also dropped into the cultures. After 10 days no fungi were found on any of this "bait."

All the significant data were obtained by the plate method. The medium used was the following:

Dextrose	10.0 grams
Peptone	2.0 grams
Agar	15.0 grams
Sea water	1000.0 cc.

This gave a reaction of pH 6.1.

In plating out, samples were taken from the supernatant water, the surface, the middle, and the bottom of the core. The water was distributed, undiluted, among five dishes and the medium added. Five samples were taken from each of the three regions of the core. These were mixed with 1 cc. of sterile water and plated out in the usual manner. Each of the mud samples was about the size of a pea and weighed 200–250.0 mg. In many cases pieces of mud were also laid on the solidified medium, but these dishes merely told whether or not fungi were present on or near the face of the sample. Flasks of unsolidified media were also tried but these became too heavily overgrown with bacteria and protozoans to be of value. As controls for each core, five plates of media were used to each of which was added the contents of a 1 cc. sterile water blank. While these were the actual controls, it will be seen that the ten dishes containing material from the middle and bottom of the core also acted as checks against laboratory contamination.

Table I gives the results of the plating out of the mud samples.

The fungi recovered from the muds by the methods outlined all belonged to genera commonly found in land soils and easily recovered in spore form from the atmosphere. A large majority were species of *Penicillium,* while others belonged to such genera as *Cephalosporium, Trichoderma, Aspergillus, Chætomium, Alternaria, Cladosporium,* and even *Rhizopus.* It was soon evident that no fungi which could be considered characteristically marine were being recovered by these methods and interest in them, qualitatively at least, was greatly diminished.

A preliminary experiment was also carried out to determine whether such fungi might be associated with decaying phytoplankton. Using a sterilized net, two sterilized jars were filled with a heavy concentration of phytoplankton from Vineyard Sound. The material was distributed equally between two sterilized battery jars, both of which were then placed under running sea water in the laboratory. By allowing the water to flow very gently into one jar (" A ") the mass of diatoms soon rested on the bottom. Since the control jar (" B ") was subjected to a stronger stream, the material was soon washed out. After four days, during which time the phytoplankton had gradually disintegrated, five 1 cc. samples were plated out from the bottom of each of the jars. Five

TABLE I

Showing the depth and number of cores taken from the stations as well as the number of samples used, their origin and the number of colonies of fungi recovered.

Origin of samples			Water above core		Surface of core		Surface of core + 1 cc. H_2O blank		Middle of core + 1 cc. H_2O blank		Bottom of core + 1 cc. H_2O blank		Control dishes	
Station	Depth	No. of cores	No. of samples	Colonies of fungi	No. of samples	Colonies of fungi	No. of samples	Colonies of fungi	No. of samples	Colonies of fungi	No. of samples	Colonies of fungi	No. of dishes	Colonies of fungi
	meters													
1	18.0	3	15	22	5	1	15	49	15	0	15	1	15	1
2	32.7	4	20	12	15	20	20	59	20	1	20	1	20	1
3	163.6	2	10	17 [1]	10	16	10	22	10	0	10	0	10	0
4	220.0	1 [2]	5	8 [3]	—[4]	—	10	11	10	0	10	1	10	0
5	1127.2	1	5	0	—	—	5	0	5	0	5	1	5	0
6	718.0	1	5	0	—	—	5	2	5	3	5	0	5	0
Totals.....		12	60	59	30	37	65	143	65	4	65	4	65	2

[1] Water very muddy and probably represents fungi from the top layer as well as in water above it.
[2] Two cores were collected but one was discarded because of the possibility that contamination had occurred.
[3] Two of these colonies were at the edge of the dish and were probably contaminations.
[4] There was not sufficient material from Stations 4–6 to use pieces of surface mud alone.

dishes of medium alone acted as controls. Sixteen colonies of fungi were recovered from jar " A " which contained the phytoplankton, and none from jar " B " which contained only the running water. The control plates remained sterile. It was apparent in this case, at least, that there existed a definite relationship between the presence of disintegrating phytoplankton and the moulds. Again, as in the muds, the fungi recovered were all common dust-borne species.

Discussion

From the foregoing, which it must be emphasized is a very preliminary investigation intended more to stimulate further inquiry than to arrive at definite conclusions, certain points seem worthy of further consideration.

If truly marine fungi of a filamentous type exist in the marine muds studied and if there is nothing radically wrong with the methods and type of medium employed, then these organisms must be extremely rare. The types of fungi recovered, i.e., species of *Aspergillus, Penicillium, Trichoderma,* etc., have cast doubts on their being concerned to any great extent in disintegrating processes in the sea. Proof of their presence in marine muds does not mean that they are in an active vegetative state and hence, a working factor in the cycle of decomposition. To the writer's mind, large numbers of direct microscopic observations of mycelium in mud seem the only positive method of demonstrating this important point. The failure of the water cultures to produce saprophytic fungi is also in line with the negative aspects of the data. However, the scanty evidence afforded by the plates of disintegrating phytoplankton presents a more positive picture of relationship. Furthermore, in direct microscopic observations on this disintegrating algal material where freedom from opaque, inorganic matter greatly facilitated the search, active septate mycelium was found in several instances.

Since only land and dust-borne fungi have been recovered it is natural to ask whether they are only contaminants or whether they are actually in the mud. In the collection of the cores every precaution against outside contamination possible with the apparatus was employed and before using the cores the mud surfaces in contact with the tube and the water were cut away. Contamination during culture procedure does not seem likely since mud from the middle and bottom of the cores yielded under identical laboratory manipulation a total of eight colonies in 130 samples and the 65 control plates two. When we consider that 239 colonies developed in the 155 dishes containing samples of supernatant water or mud from the top layer of the core it would seem fairly conclusive that the fungi recovered were actually present in the mud.

Two methods whereby the moulds may have reached the muds are suggested. Either they have been washed from land soils into the sea, or they have been blown, in spore form, from land onto the surface of the water where they have gradually sunk to the bottom. While the stations studied were not in the littoral zone, none was sufficiently offshore to be free from the possibility of obtaining spores from sedimentary material of land origin. Spores are known to be everywhere in the lower atmosphere, and in the immediate vicinity of a continent would be particularly abundant. Many of these would eventually reach the surface of the sea where they might ultimately sink to the bottom. In this connection, qualitative studies (unpublished) by Miss Lois Lillick of the phytoplankton of Vineyard Sound and the Gulf of Maine show that in the former locality fungous spores occur generally throughout the year in the samples, and that they also occur in the shallower waters of the Gulf of Maine, particularly during April and May. It is entirely possible, therefore, that either or both methods of conveyance have contributed fungous material to the marine muds.

Perhaps the most interesting feature of the present investigation has been the information added to our knowledge of the vertical distribution of these ubiquitous moulds. Many types have been recovered from the atmosphere both over land masses and the ocean and even in the stratosphere. Land soils and fresh water have yielded fungi and now they have apparently been recovered in some viable form from the surface of the ocean floor at depths up to 220 meters. Such hardihood is not surprising to those who have observed the capacity of certain of these fungi to withstand adverse environmental circumstances and even to produce under these conditions active vegetative growth.

Finally, it might be emphasized that while no typically marine fungi were found there is strong evidence for believing that certain soil and dust-borne fungi can exist in the surface muds although it has not been shown in what form they occur or that they take an active part there in the disintegration of organic materials.

Summary

Stratified samples of marine bottom were collected under as sterile conditions as possible from four stations which varied from 18 to 220 meters in depth. These stations were located in Buzzard's Bay, Vineyard Sound, and the Gulf of Maine and varied considerably in their distances from land. Attempts were made to recover saprophytic fungi from these cores. Two methods were used: (1) water cultures "baited" with suitable material of marine origin; and (2) the plating out of samples from (*a*) the water immediately above the surface of

the mud core, (*b*) the surface of the core, (*c*) the middle, and (*d*) the bottom of the core. Suitable controls were maintained. No fungi were found in the water cultures. By the plate method using a nutrient medium made up in sea water, 239 colonies were formed in dishes containing water from just above the surface of the core and from the surface of the core itself, eight colonies, in dishes containing material from the middle and bottom of the core, and two colonies in the controls.

A preliminary experiment to determine whether or not fungi were associated with decaying phytoplankton showed definitely that such was the case.

The fungi obtained by the plate method were all common dust and wind-borne forms. Since the methods used in the recovery of fungi did not show in what form they existed on the sea-bottom and since no species which might be called typically marine were recovered, it is doubtful in the present state of our knowledge whether these organisms play an active part in the disintegration of organic materials present in the mud.

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Contribution No. 91

SOME GEOGRAPHICAL RESULTS OF THE SECOND BYRD ANTARCTIC EXPEDITION, 1933-1935

I

THE SUBMARINE TOPOGRAPHY OF THE ROSS SEA AND ADJACENT WATERS*

S. Edward Roos

THE oceanographic program of the Second Byrd Antarctic Expedition, which left Boston in the latter part of September, 1933, included a systematic bathymetric survey in the form of echo soundings begun as soon as the Pacific Ocean was entered.

Soundings were taken hourly, i.e. about seven miles apart. However, when any outstanding change in the bottom configuration was encountered, or when a continental or insular shelf was approached and left, the soundings were increased to any number required to obtain the detailed profile of the bottom. In all, ten series, totaling 2723 soundings, were carried out by the *Bear of Oakland* during her various cruises.[1] They are: Panama to Tahiti; Tahiti to New Zealand (North Island); Dunedin, N. Z., to the Bay of Whales, Ross Sea; an exploratory cruise to the waters northeast of King Edward VII Land; a cruise across the Ross Sea to latitude 72° S. for a rendezvous with the R.R.S. *Discovery II*; Bay of Whales to Dunedin, N. Z.; Dunedin, N. Z., to the Bay of Whales (including the Scott Island Rise, western sector of the Ross Sea, and front of the Ross Shelf Ice); Discovery Inlet, Ross Sea, to Dunedin, N. Z.; Dunedin, N. Z., to Easter Island; Easter Island to the Gulf of Panama.

The soundings fall into two main divisions: the trans-Pacific series and the series related directly to the Antarctic. The present paper deals chiefly with the latter;[2] for the former see Appendix II.

The Sections: South of New Zealand

In general, the bottom contours crossed by the *Bear* on her four passages between New Zealand and the Ross Sea have an east-west trend. The most conspicuous feature of the sections is the pronounced

*Constituting *Contribution No. 91* of the Woods Hole Oceanographic Institution.

The writer wishes to express his gratitude to Mr. C. O'D. Iselin 2nd, counselor and guide in the preparation of the sounding data. All positions were determined by Lieutenant R. A. J. English, U.S.N., commanding the *Bear of Oakland*, for whose invaluable assistance the writer is greatly indebted.

[1] Photostats of the tabulated soundings have been distributed to the various hydrographic agencies. Additional copies can be obtained by request from the Woods Hole Oceanographic Institution, Woods Hole, Mass.

[2] A line of echo soundings between Dunedin, N. Z., and the Bay of Whales was obtained on the First Byrd Antarctic Expedition. These soundings are plotted, uncorrected, on the map of the routes of the *City of New York*, Plate II in W. L. G. Joerg: The Work of the Byrd Antarctic Expedition 1928–1930, Amer. Geogr. Soc., 1930.

[Reprinted from *The Geographical Review*, Vol. XXVII, No. 4, October, 1937.]

FIG. 1 (above)—Bathymetric map of the Ross Sea and adjacent waters; scale approximately 1 : 35,000,000. The map revises that part of the American Geographical Society's Bathymetric Map of the Antarctic (1 : 20,000,000), 1929. In addition to the soundings obtained by the *Bear* use has been made of the echo soundings by S. Y. *Discovery*, B. A. N. Z. Antarctic Expedition (Mawson), 1929, 1930, 1931, in "List of Oceanic Depths Received at the Admiralty during the Year 1932," *Publication H. D. 308*, London, 1933; soundings by R. R. S. *William Scoresby*, 1928, in *Discovery Reports*, Vol. 3, pp. 1–134 (Ross Sea soundings, pp. 124–131), 1930; soundings by R. R. S. *Discovery II*, 1932, in "List of Oceanic Depths . . . 1932"; soundings by *Thorshavn*, 1933–1934, list sent by H. E. Hansen, Norges Geografiske Opmåling.

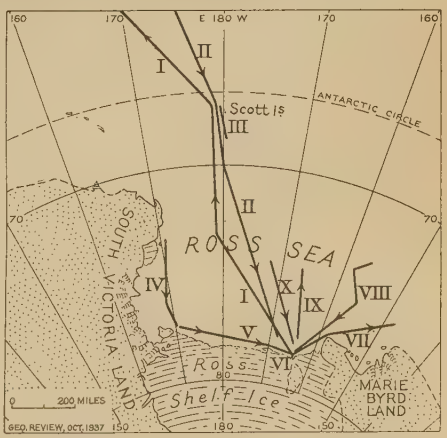


FIG. 2 (right)—Index map to the profiles in the Ross Sea and neighboring waters. Scale 1 : 40,000,000.

ridge with its crest in 64° S. It is, in fact, a westward extension of the Easter Rise and separates the South Pacific Basin from the Pacific Antarctic Basin. The soundings from two of the sections are plotted in Figure 3.

The profiles (Fig. 3) show the New Zealand insular shelf receding

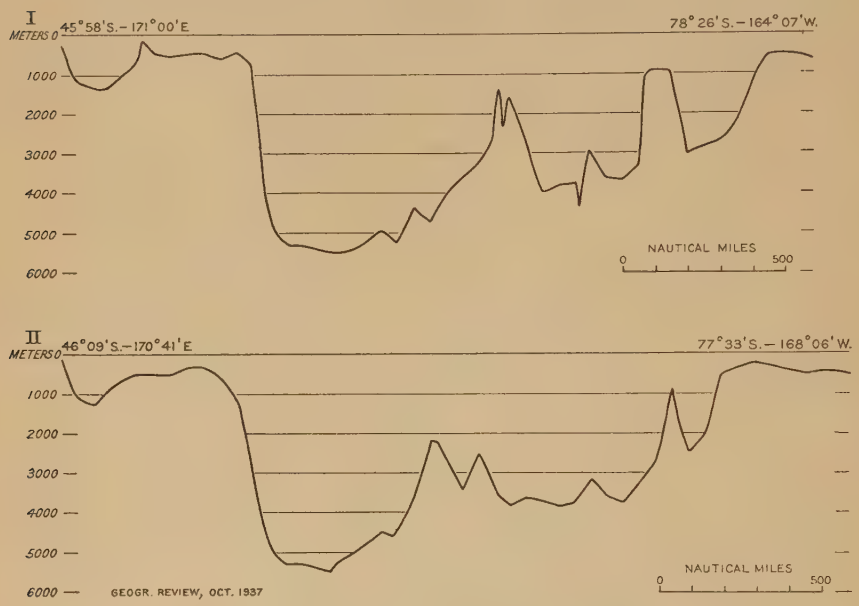


FIG. 3—Profiles I and II, New Zealand–Bay of Whales.

in a very steep slope to 5000 meters about 500 miles[3] south of the starting point, Dunedin. The trend of this contour on the chart (Fig. 1) indicates that the South Pacific Basin extends far to the southwest, possibly terminating at Macquarie Island. The maximum depth of water found by the *Bear* when crossing this deep tongue was 5500 meters; the bottom remained deeper than 5000 meters for a distance of 300 miles, until, at first gradually and then with greater incline, it shoaled to form the extensive rise mentioned above, the crest of which shows an elongated depression. The soundings indicate that the ridge deepens rapidly eastward. For the next 300 miles southward the depths again increase, except in the vicinity of Scott Island.

SCOTT ISLAND AND VICINITY

Scott Island, 67° 24′ S., 179° 55′ W., was discovered on Christmas Day, 1902, by the relief ship *Morning*, Captain Colbeck, of Scott's National Antarctic Expedition.[4] As Figure 1 suggests, this island

[3] All miles are nautical.

[4] G. S. Doorly: The Voyages of the 'Morning,' New York, 1916, pp. 58–62.

might well be called the boundary stone between the South Pacific and the Ross Sea.

Figure 4 shows the profile obtained on the second cruise of the *Bear*, season 1934–1935. The bottom rises steeply from a depth of 3800 meters for a distance of 12 miles to emerge as a rocky island about 175 feet in height, with precipitous sides, crowned with the characteristic Antarctic icecap, which extends seaward in a southeasterly direction. This shelf-ice formation was not apparent when the island was sighted—the second time since its discovery—by the First Byrd Antarctic Expedition in December, 1928.

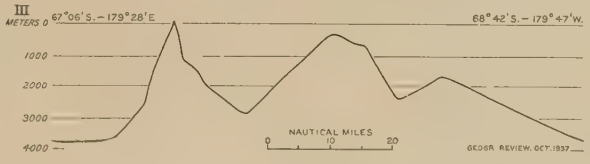


FIG. 4—Profile III, Scott Island, based on 35 soundings.

The near-by jagged peak of Haggitt's Pillar is really a part of Scott Island. Just south of Scott Island the bottom recedes steeply to 2900 meters, then rises again to 300 meters within 25 miles of the island. One may believe that this peak culminates in rocks awash. However, no breakers were observed from the deck of the *Bear*.

THE ISELIN AND PENNELL BANKS

About 200 miles south of Scott Island the *Bear's* soundings disclosed a heretofore unknown ridge, at a minimum depth of 700 meters, separated by a deep gully from the Antarctic continental shelf (see Fig. 3), which here rises with a steep gradient from a depth of 2800 meters. The discovery of this ridge, which has been named the Iselin Bank after Mr. C. O'D. Iselin 2nd of the Woods Hole Oceanographic Institution, is of interest in relation to the hypothesis of a structural connection between New Zealand and West Antarctica, comparable to the Scotia Arc postulated as a link of the Antarctandes.[5] The axis might run from the Alexandra Mountains by way of the Pennell Bank,[6] the Iselin Bank, Scott Island, and Macquarie Island to the New Zealand shelf. There are deep water gaps between these links, as there are between links of the Scotia Arc, but this objection is not insuperable. However, many more soundings are needed before any definite conclusions can be drawn.

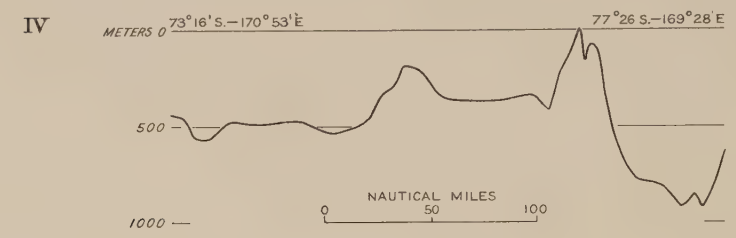
The Pennell Bank extends southeast to northwest across the Ross Sea. The suggestion of Griffith Taylor that the bank represents a vast terminal moraine[7], a remnant from the maximum glaciation, has

[5] For a discussion of the problem of the Scotia Arc see H. F. P. Herdman: Report on Soundings Taken during the Discovery Investigations, 1926–1932, *Discovery Reports*, issued by the Discovery Committee, Colonial Office, London, Vol. 6, pp. 205–236, Cambridge, 1932.

[6] An alternative course would be from the Pennell Bank via the Balleny Islands.

[7] Griffith Taylor: Antarctic Adventure and Research, New York and London, 1930, p. 160.

been further strengthened by the results of the dredging carried out from the *Bear*. After all the hauls the dredges were recovered filled with rocky bits of glacial debris. They were chiefly acid igneous rocks, though there were occasional fragments of the more basic varieties; sedimentary rocks were represented by small quantities of



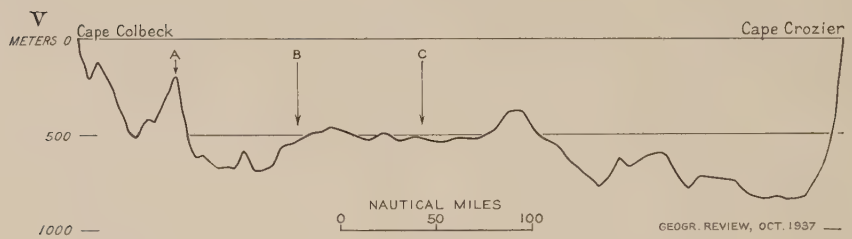


FIG. 5—Profile IV, Coulman Island to Ross Island, based on 57 soundings.

FIG. 6—Profile V, along the front of the Ross Shelf Ice, based on 151 soundings. A, eastern junction of the Shelf Ice; B, Bay of Whales; C, Discovery Inlet.

green shale and friable sandstone. When the *Bear* was leaving the Ross Sea in 1935, a shallow with a minimum depth of 134 meters was observed on the Pennell Bank in 74° 11′ S., 179° 43′ E. A bottom sampler was lowered at this point, where the bank tends to turn northward; however, the corer was recovered dented, an indication that it had struck a hard or rocky surface.[8]

Western Sector of the Ross Sea and the Shelf Ice

The profile reveals an irregular submarine topography in the western sector of the Ross Sea (Fig. 5). In the southwest is a depression bordered on the north by the Pennell Bank and interrupted by Franklin Island, a small volcanic island. Although separated from them by a gully with a depth of 900 meters, this island is structurally related to Ross Island, to the south, and Coulman Island, to the north.

Figure 6 is a profile parallel to the face of the Ross Shelf Ice from Cape Crozier, on Ross Island, to Cape Colbeck, King Edward VII Land. The slopes of Ross Island recede steeply to 850 meters; and

[8] See also the note on "Bottom Deposits of the Ross Sea" elsewhere in this number of the *Geographical Review*.

for a distance of 150 miles eastward the bottom remains at a depth of about 600 to 750 meters—an indication that the depression continues under the shelf ice. Farther to the east the bottom rises markedly to the lowest recorded depth of 352 meters. The profile shows another drop, to about 700 meters, at the Bay of Whales (Fig. 6), where an arm of deeper water penetrates into the Pennell Bank.

The probability that the Ross Shelf Ice is resting on the bottom at any point along its front seems remote, though evidence seems to

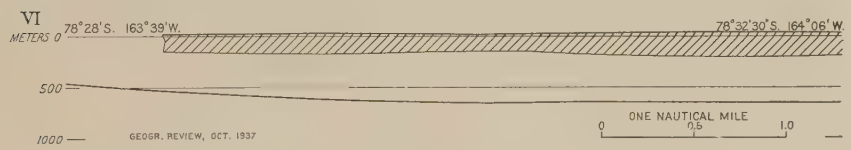


FIG. 7—Profile VI, the floor of the Bay of Whales showing the extension of the shelf ice in relation to the bottom as observed January, 1935. Vertical and horizontal scales equal.

indicate that it does so farther south.[9] The minimum depth of 352 meters, shown in Figure 6, was obtained at a point (78° 19′ S., 172° 56′ W.) where the altitude of the barrier above the sea level was about 80 feet, and this would seem, by reason of the buoyancy of the ice alone, to indicate that the edge is afloat. The floor of the Bay of Whales and its relation to the ice as observed January, 1935, are shown in Figure 7. A wire sounding taken while the ship was moored to the barrier on the east side of Eleanor Bolling Bight gave a depth of 642 meters, and one taken three miles farther south while the ship was moored to the bay ice gave a depth of 644 meters. In neither case was there any wire angle noted. A depth of 480 meters was recorded half a mile off West Cape and also at the eastern extremity of the bay, and a depth of 492 meters half a mile off the eastern extremity. Should any point of the shelf ice be grounded in this region, it must be on a pinnacle, or pinnacles, rising steeply from the gentle southward slope. In the region just north of the Bay of Whales the bottom rises to a minimum depth of 179 meters.

NORTHEASTERN SECTOR OF THE ROSS SEA

In 1934 the northeastern sector of the Ross Sea remained a virgin field as regards submarine topography. Soundings on a line from the Bay of Whales to Cape Colbeck and beyond (Fig. 8) were begun as soon as the eastern extremity of the bay was cleared. There is no distinguishing mark or point that can properly be called the east cape. The barrier here curves eastward in a wide sweep, and the extremity of the bay was judged by the visibility of the bay ice and the bearing of the west cape. After the ship had crossed the deep

[9] L. M. Gould: The Ross Shelf Ice, *Bull. Geol. Soc. of America*, Vol. 46 (Part 2), 1935, pp. 1367–1393.

tongue penetrating into the Pennell Bank toward Cape Colbeck, the bottom began to rise gently. It culminated in a ridge at a minimum depth of 89 meters (76° 51′ S., 157° 15′ W.), on which were a great number of stranded icebergs. Through their general direction the ridge could be traced, trending in a northwesterly direction, seemingly as if the Alexandra Mountains were continued beneath the

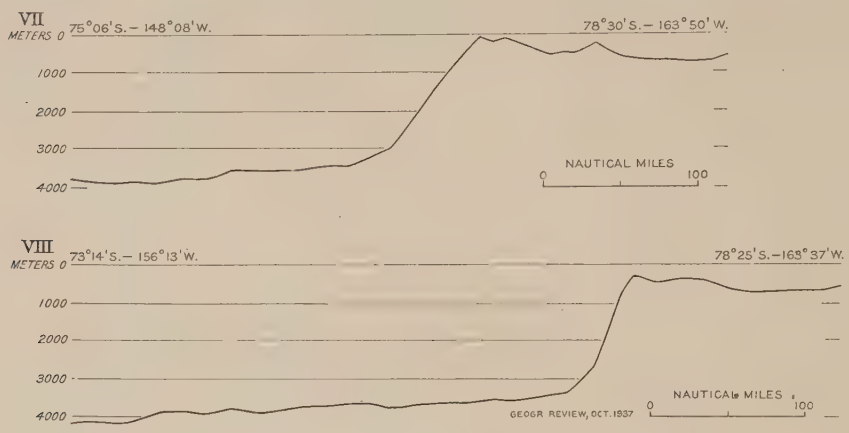


FIG. 8—Profiles VII and VIII, northeastern sector of the Ross Sea.

surface of the sea. From this narrow beginning the bank broadens as it continues across the Ross Sea.

The isobaths east of Cape Colbeck have heretofore been drawn on the assumption that here is a broad continental shelf. However, when the spur off Cape Colbeck had been passed, it was found that the bottom at once receded steeply to 3500 meters, then remained level at 3800 meters for the distance traversed by the *Bear*. While on this section, the ship was forced to alter her course to the north after reaching the farthest east in 75° 6′ S., 148° 8′ W. However, the soundings were continued while the ship was navigating in or skirting the pack ice. The whaling factory ship *Thorshavn* reached a position of 71° 44′ S., 134° 11′ W., on February 10, 1934, and reported a depth of 3722 meters.[10] From this position a flight was made to 72° 8′ S., from which was obtained "a clear sight of the ice barrier about 35 miles south."[11] This would support the belief that the lands in the wide unknown expanse to the south consist of islands locked in an ice-shelf formation similar to the Ross Shelf Ice. In conjunction with the westerly current this also explains the presence off Cape Colbeck of the great number of huge tabular and peculiarly dome-shaped icebergs grounded there.

[10] This is the corrected depth (2204 fathoms) in "List of Oceanic Depths," 1936, Publ. H. D. 327, Hydrographic Dept., Admiralty, London, 1937; see p. 18.

[11] Manuscript report received by the American Geographical Society from Consul Lars Christensen. This may have been only the edge of a large tabular iceberg.—EDIT. NOTE.

These observations remove any doubt that the continental land east of the Ross Sea extends conspicuously northward. The southern limit of the Pacific Antarctic Basin is brought farther to the south and can be separated from the coast by only a narrow strip of continental, or perhaps insular, shelf.

The *Bear* reached her farthest north in 73° 14′ S., 156° 13′ W., and the course was altered to return to the Bay of Whales. Profile VIII (Fig. 8) shows the gentle southward rise of the Pacific Antarctic

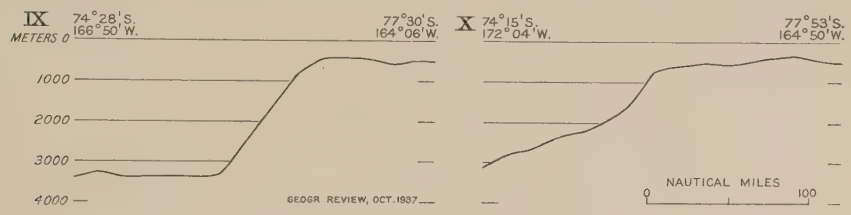


FIG. 9—Profiles IX and X, in the Ross Sea from cruise for rendezvous with the *Discovery II*.

Basin and the steep, almost precipitous slope to the Pennell Bank and the Antarctic shelf. Because of the uniformity of the deeps in the eastern sector of the Ross Sea—which contrasts with the irregularities of the western sector—curiosity was aroused concerning a shallow of 117 meters in 74° 45′ S., 164° 18′ W. shown on the international bathymetric charts. A line of soundings run parallel to the 165th meridian west (Fig. 9) while the *Bear* was en route to a rendezvous with the R.R.S. *Discovery II* revealed depths between 3382 and 3660 meters in these waters.[12]

The floor of this section, bordered on the south by the narrow continental shelf and the Pennell Bank and on the north by a continuation of the great Easter Rise, is a depression. Yet it is not impossible that rocky islands exist therein. Submarine and subaerial volcanic activity is known, and precipitously rising cliffs are not uncommon. One need mention only Scott Island, to the west, and Peter I Island, to the east, as examples.

APPENDIX I—EQUIPMENT AND METHODS

The *Bear* was equipped with a fathometer, of unlimited depth range, manufactured by the Submarine Signal Company of Boston, Mass., before our departure. On a ship of such unusually heavy construction as the *Bear*, an old icebreaker, the installation of the hydrophone and oscillator must differ considerably from the installation on the usual steel ship. The hydrophone tank, containing a deep hydro-

[12] Subsequent communication with the International Hydrographic Bureau, Monaco, in regard to this revealed that the shoal shown on the chart and also a number of other soundings south of this were plotted on the second edition (1912–1925) of the "Carte générale bathymétrique des océans," Sheet C'II, in west longitudes, whereas the longitudes should have been east. These soundings should, therefore, appear on Sheet C'III. They will thus be found located close to the coast of South Victoria Land. The longitudes are correctly given in Part 3 (1914) of the publication "Carte générale bathymétrique des océans," p. 218, and in the "List of Oceanic Depths," 1911, published by the Hydrographic Department of the Admiralty, London, 1912, p. 23.

phone, Type 341 A, was placed in the starboard garboards 3 feet from the keel, where a hole with a diameter of 8 inches had been cut through the planking. The tank was fitted and bolted to the hull so that a part of it protruded 8 inches outside. Around this protruding part was constructed a wooden fore-and-aft fairwater so as to eliminate as much as possible the noises created by the ship's headway. The oscillator, deep Type 324 ("pancake" type), located 12 meters aft of the hydrophone, was set in a heavy steel casting bolted through the hull. Here also wooden fairwaters were constructed. Both instruments were so placed that they would be clear of any ice that might wash downward. To prevent freezing, the hydrophone tank was filled with a solution of equal parts of sea water and an antifreeze mixture.

The sounding unit, operating on a frequency of 525 cycles, was controlled in the laboratory, located below deck off the wardroom aft. The equipment installed did not include an indicator, or automatic timing device, which is usually a part of the fathometer. The outgoing signal was controlled by a key, and the returning echo was received in earphones, the volume being adjusted by an amplifier. The timing was done with delicate, 1/100-second Longines stop watches.

A table converting the time elapsed into depths in meters was constructed based on a sounding velocity of 1500 meters a second (820 fathoms). The stop watches were checked from time to time against the ship's chronometers, but no errors were detected. Steps were taken to guard against error. An average of three series of three soundings each was usually accepted as the depth to be recorded. Allowance was made for personal error, ascertained by constant checking against known depths. On the voyage from Norfolk, Va., to Panama ample opportunity was offered to compare the recorded depths with known depths in well surveyed waters.

A puzzling feature was an inexplicable sudden weakening of the echoes. Soule and Ennis wrote concerning their observations on board the *Carnegie*:[13] "The weakness of the returning echo was a puzzling element which sometimes made sounding difficult—puzzling in its seeming independence of slope, type of bottom, or depth."

The phenomenon was particularly noted in the little-surveyed area of the sub-Antarctic waters between the New Zealand insular slope and Scott Island (67° 24′ S., 179° 55′ W.). The condition of the bottom may have had something to do with this: it is generally believed that a soft bottom has a tendency to return a weak echo. Another explanation may be that, when the rolling of the ship produces an excessive angle between the ocean floor and the face of the hydrophone tank, the incoming echo perhaps is less audible.

For correcting the soundings the British Admiralty tables[14] were used. The tables had to be extended by extrapolation for the deeper waters in their regions 13, 16, and 20. The boundary between regions 20 and 23 along the lines southward from New Zealand could be determined on the basis of surface temperature readings made from the *Bear*. As an average value for draft, 5 meters has been added to each sounding.

Appendix II—The Trans-Pacific Profiles

For completion of the record the trans-Pacific profiles obtained by the *Bear* are given here without discussion.

Profile XI (Fig. 10) was begun off Punta Mala, Panama, and concluded off Tahiti, Society Islands. This fairly well known sector had previously been surveyed by echo-sounding lines from several vessels, notably the *Ara* and the *Carnegie*, Cruise VII.

[13] F. M. Soule and C. C. Ennis: Sonic Depth-Finding on the Carnegie, Cruise VII, *Trans. Amer. Geophys. Union, Tenth Ann. Meeting, April 25 and 26, 1929, Eleventh Ann. Meeting, May 1 and 2, 1930*, Washington, 1930, pp. 264–274: reference on p. 269.

[14] Tables of the Velocity of Sound in Pure Water and Sea Water for Use in Echo-Sounding and Sound-Ranging, *H. D. 282*, Hydrographic Dept., Admiralty, London, 1927.

Profile XII (Fig. 11) was run over a part of the deepest region of the South Pacific. The soundings that have been taken in this region, chiefly those of the *Challenger*, are few and far between. Of outstanding interest is the discovery of the two pinnacles or ridges (*B* and *B'*), in the so-called Aldrich Deep. The deepest readings

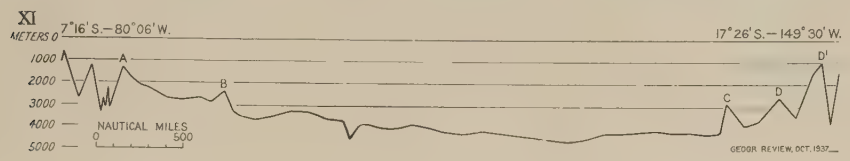


FIG. 10

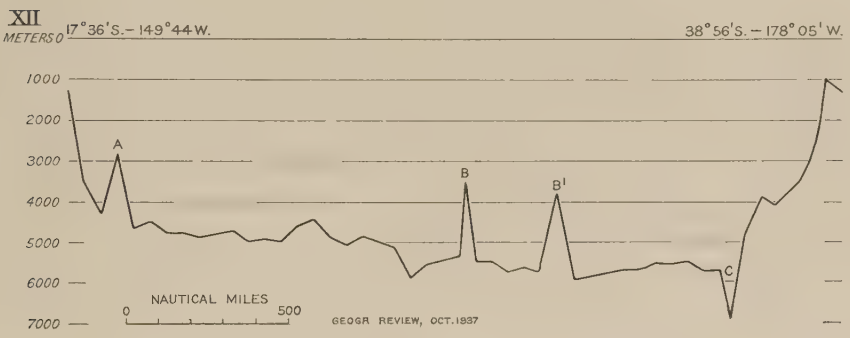


FIG. 11

FIG. 12

FIG. 10—Profile XI, Punta Mala, Panama, to Tahiti, Society Islands. A, Cocos Island shelf; B, Galapagos Islands shelf; C, indications of Marquesas shelf; D-D', Tuamotu shelf.

FIG. 11—Profile XII, Tahiti, Society Islands, to New Zealand. A, Cook-Austral ridge; B-B', pinnacles or ridges in the so-called Aldrich Deep; C, Kermadec Deep.

FIG. 12—Profile XIII, New Zealand to Easter Island. A, Bounty-Antipodes ridge. Dotted line indicates lack of soundings.

shown in the profile are identified as the south end of the Kermadec Deep, which, apparently, curves toward the southeast in this sector.

Profile XIII (Fig. 12), New Zealand to Easter Island, crosses a region that has hitherto been a part of the greatest unknown area of the Pacific Ocean. Our previous knowledge of the submarine topography of this region was based chiefly on the line of soundings along the 50th parallel carried out by the U.S.S. *Enterprise* during a trans-Pacific crossing in 1884. As will be noted by comparing this profile with that of Figure 11, the South Pacific Basin deepens considerably to the south before reaching its southern border, the Easter Rise.

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GEOPHYSICAL INVESTIGATIONS IN THE EMERGED AND SUBMERGED ATLANTIC COASTAL PLAIN

PART I: METHODS AND RESULTS

BY MAURICE EWING, A. P. CRARY, AND H. M. RUTHERFORD

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INTRODUCTION

This report describes the development and application of a seismic method of procedure for making studies of submarine geology. Any new tool for gaining information about the submerged portion of the earth's crust would be noteworthy because few such tools are available. The present method merits additional consideration because its findings are directly translatable into such concrete terms as depth to certain horizons in the rocks and the elastic constants of the rocks.

In the seismic method, elastic waves, which are produced by means of explosives, travel through the upper layers of the earth to seismographs or geophones, which serve to measure the travel-time of the waves. In the seismic reflection method, the elastic waves studied are those that have gone almost directly downward and have returned to the surface as echoes from subterranean discontinuities. In the seismic refraction method, the waves studied are those that have penetrated to a zone in which their velocity is relatively high and have returned to the surface after traveling horizontally for considerable distance in this zone.

In the present extension of these methods of investigation to submarine problems, both the charge of explosive and the geophones were placed on the ocean floor, but in other respects the method of operation was similar to that used on land. Both reflection and refraction methods were used successfully, but the more important results came from the refraction measurements.

In its present state of development, the method is not applicable in water deeper than about 100 fathoms, or, in other words, beyond the edge of the continental shelf. For working in deeper water, additional seismic equipment and a ship capable of handling long heavy cables are needed. Preliminary designs for the necessary apparatus have been made. The equipment needed would be expensive, the demands upon operating technique great, and the rate of accumulation of data slow, but the results should be of sufficient interest to justify the effort.

The locations at which measurements were made are shown in Figure 1. In addition to four stations at sea south of Woods Hole, Massachusetts, a fairly complete section across the submerged and emerged portions of the Atlantic Coastal Plain at Cape Henry, Virginia, have been studied by the refraction method. These studies classified the subsurface materials into three zones: unconsolidated sediments, semi-consolidated sediments, and crystalline rocks; both the thickness and the velocity of longitudinal elastic waves in each zone were determined.

Seismic reflection tests were made at scattered points along the Cape Henry section, and numerous reflections of good quality were obtained. As the reflection stations were spaced several miles apart, it has been impos-

sible to correlate the various reflecting horizons from station to station. However, the reflection studies have definitely proved that good reflections

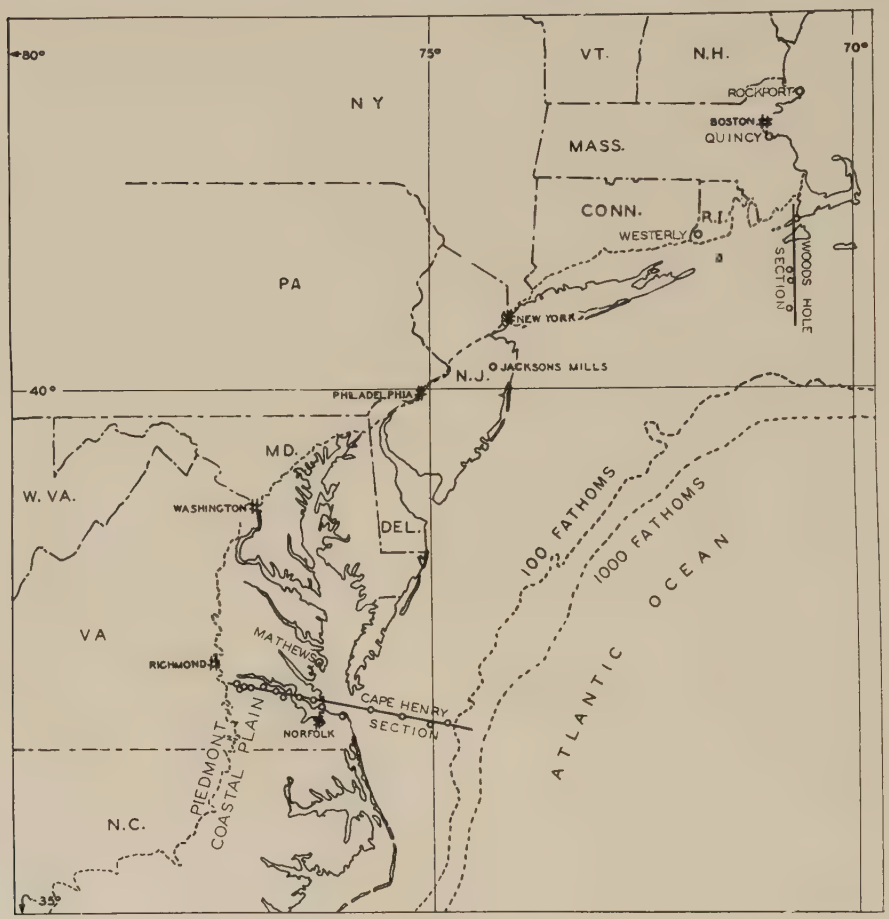


FIGURE 1.—*Key map of regions studied*

may be obtained in several hundred feet of water, and they have given qualitative corroboration of the depth to crystalline rocks—a determination deduced from refraction tests.

ACKNOWLEDGMENTS

The writers are indebted to the Geological Society of America, the Woods Hole Oceanographic Institution, and the United States Coast and Geodetic Survey for generous and substantial contributions of funds and facilities, without which the project could not have been undertaken.

The willingness of officials of Lehigh University and the University of Pittsburgh to grant leave of absence for making the cruise on the *Atlantis* is greatly appreciated.

The Geophysical Research Corporation loaned the geophones used in the work and gave valuable cooperation in several other instrumental problems.

C. O. Iselin and H. C. Stetson gave much assistance in perfecting the technique of refraction measurements, and the officers of the *Oceanographer* and of the *Atlantis* made every effort to facilitate the work. William Bowie, N. H. Heck, R. M. Field, and B. L. Miller gave valuable assistance and encouragement at every stage in the development of the project.

HISTORICAL BACKGROUND

The earliest published discussion of the feasibility of studying submarine geology by the seismic method is probably that by DeGolyer [1] in the symposium on the "Application of Geophysics to Ocean Basins and Margins," held at the annual meeting of the American Geophysical Union in 1932. Since then, the application of the seismic method has been prominent among the projects receiving attention of the Committee on Geophysical and Geological Study of Oceanic Basins,[2] of the American Geophysical Union, whose chairman, R. M. Field, has been an able leader in the study of submarine geology.

Reflection and refraction measurements were made in water-covered areas as early as 1927 for the purpose of locating oil-bearing structures.[3] Ewing and Rutherford took part in a survey of the coastal lakes of Louisiana in 1928. The experience gained in working in water 5 to 20 feet deep proved valuable in the present project. In the previous work, the geophones were planted securely in lake-bottom mud by the use of long poles (a procedure not feasible at sea); the recording instruments were carried in launches capable of executing maneuvers impossible for ships to perform; and distances were obtained by measuring travel-times of air waves. Hence, it seems reasonable to classify the measurements made in the lakes and bayous of the Gulf Coast in the same group with land operations, and to consider the present work the initial application of seismic measurements to submarine geological problems.

The field measurements herein described were made by the present writers, who had the benefit of the advice of B. L. Miller on geological

[1] Everett DeGolyer: *The application of seismic methods to submarine geology*, Am. Geophys. Union, Tr. (1932) p. 37.

[2] R. M. Field: *Report of committee on geophysical and geological study of oceanic basins*, Am. Geophys. Union, Tr. (1933) p. 13; (1935) p. 6; (1936) p. 8.

[3] E. E. Rosaire and O. C. Lester, Jr.: *Seismological discovery and partial detail of Vermillion Bay salt dome, Louisiana*, Am. Assoc. Petrol. Geol., Bull., vol. 16 (1932) p. 1221.

questions. The first preliminary tests were made in May 1935, in the vicinity of the deep bore-hole at Jackson Mills, New Jersey (Fig. 1).

The next tests were made between June 17 and June 30, 1935, on board the ship *Oceanographer,* of the United States Coast and Geodetic Survey, which was engaged in hydrographic work off Cape Henry. It was a great privilege to be accompanied on this cruise by Captain N. H. Heck, Chief of the Division of Seismology and Terrestrial Magnetism of the United States Coast and Geodetic Survey, whose broad experience in scientific work at sea enabled him to give much valuable advice and assistance.

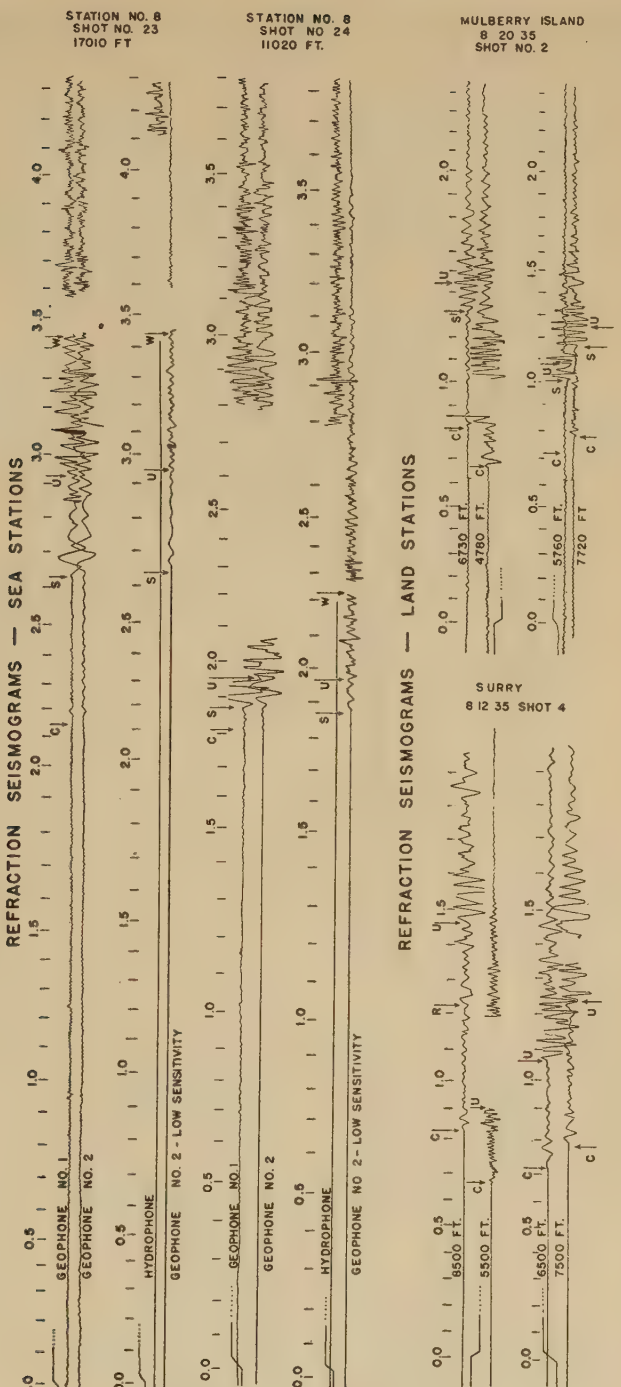
The work on the *Oceanographer* proved the feasibility of the project. It was confined to reflection tests, the most successful of which were made at night, when the ship was anchored.

Calibration tests on land by the reflection method were made from July 2 to 15 at Mathews and at Fort Monroe, Virginia, near deep wells, which extend to the crystalline rocks. It soon became apparent that one, or more, long refraction profiles were needed, and by July 25, arrangements were completed for seismic refraction work. The transmission of seismic energy by the sediments of the region was found to be phenomenally efficient, so that, although the supply of explosives was limited, many more refraction measurements could be made than had been anticipated. As refraction measurements give more complete information than do reflection measurements, and as the former are not dependent upon calibration of velocities at a point where the depth is known, the feasibility of using this type of measurement was of the greatest importance.

July 25 to August 22 was spent in making seismic refraction measurements at eleven stations between Cape Henry and Petersburg, Virginia. These formed a vital part of the work. They gave ample calibration as well as definite information about the conditions to be expected at the first stations at sea, and reduced the whole problem of working at sea to a gradual progression from the known to the unknown.

The final measurements at sea were made on the ship *Atlantis,* of the Woods Hole Oceanographic Institution. A short cruise on the *Atlantis* was made October 16 to 19, during which time, refraction measurements were made at four stations, on a line extending south from Woods Hole. These were the first refraction tests to be made at sea, and, during the development of the technique, the writers had the assistance of C. O. Iselin and H. C. Stetson, of the Woods Hole Oceanographic Institution, and of R. M. Field, of Princeton University. The data for these stations are incomplete, but, nevertheless, they afford important confirmation for certain results on the Cape Henry profile.

Actual measurements for the sea stations on the Cape Henry profile occupied the time from October 26 to 30. Four refraction stations and



REPRESENTATIVE SEISMOGRAMS

six reflection stations were occupied. Thoroughly satisfactory results were obtained at the first two refraction stations, but the amount of testing had to be curtailed at the last two stations because of a shortage in the supply of explosives. For this reason, the results at the last two stations are below the desired degree of accuracy. Excellent reflections were obtained at the six reflection stations, but the stations are so far apart that correlation of the reflecting horizons is not possible. The reflection data offer valuable qualitative support for the refraction results.

REFRACTION MEASUREMENTS ON THE CAPE HENRY SECTION

LOCATION

Refraction measurements were made at fifteen stations, on a line approximately 150 miles long, crossing the entire Coastal Plain at Cape Henry. At each station, one, or more, shot points and several recording

TABLE 1.—*Refraction Stations of the Cape Henry Section*

STATION	WEST LONGITUDE	NORTH LATITUDE	DISTANCE * (miles)
1 Camp Lee	77°20.3′	37°14.7′	3.4
2 Youngblood's Store	77°19.6′	37°10.8′	4.6
3 Prince George	77°15.0′	37°11.7′	9.0
4 Newville	77°08.9′	37°11.7′	14.4
5 Brandon	77°02.6′	37°12.9′	20.1
6 Mercy Seat Church	76°52.6′	37°08.9′	29.8
7 Surry	76°46.4′	37°05.7′	35.9
8 Mulberry Island	76°34.8′	37°06.7′	46.7
9 Hampton	76°23.9′	37°03.6′	57.0
10 Fort Monroe	76°17.9′	37°01.0′	62.7
11 Cape Henry	76°03.9′	36°54.2′	77.9
12 Station 8	75°43.2′	36°57.3′	95.3
13 Station 12	75°25.7′	36°54.2′	112.0
14 Station 16	75°01.1′	36°49.5′	135.4
15 Station 20	74°49.6′	36°49.8′	145.9

* Miles east of Petersburg, Va.

points were established, and the latitude, longitude, and elevation were obtained from topographic maps or hydrographic charts. The line representing the Cape Henry Section and the various stations that constitute the section are shown in Figure 2. Each station has been projected to this line. The distance of each projected point from Petersburg serves as a coördinate for locating the corresponding station. Data on station locations are given in Table 1.

METHOD FOR LAND STATIONS

Fifty per cent dynamite was used as a source of elastic waves. This was placed in holes, 10 to 15 feet deep, drilled with hand augers. An insulated wire, forming part of the plate circuit of a radio transmitter,

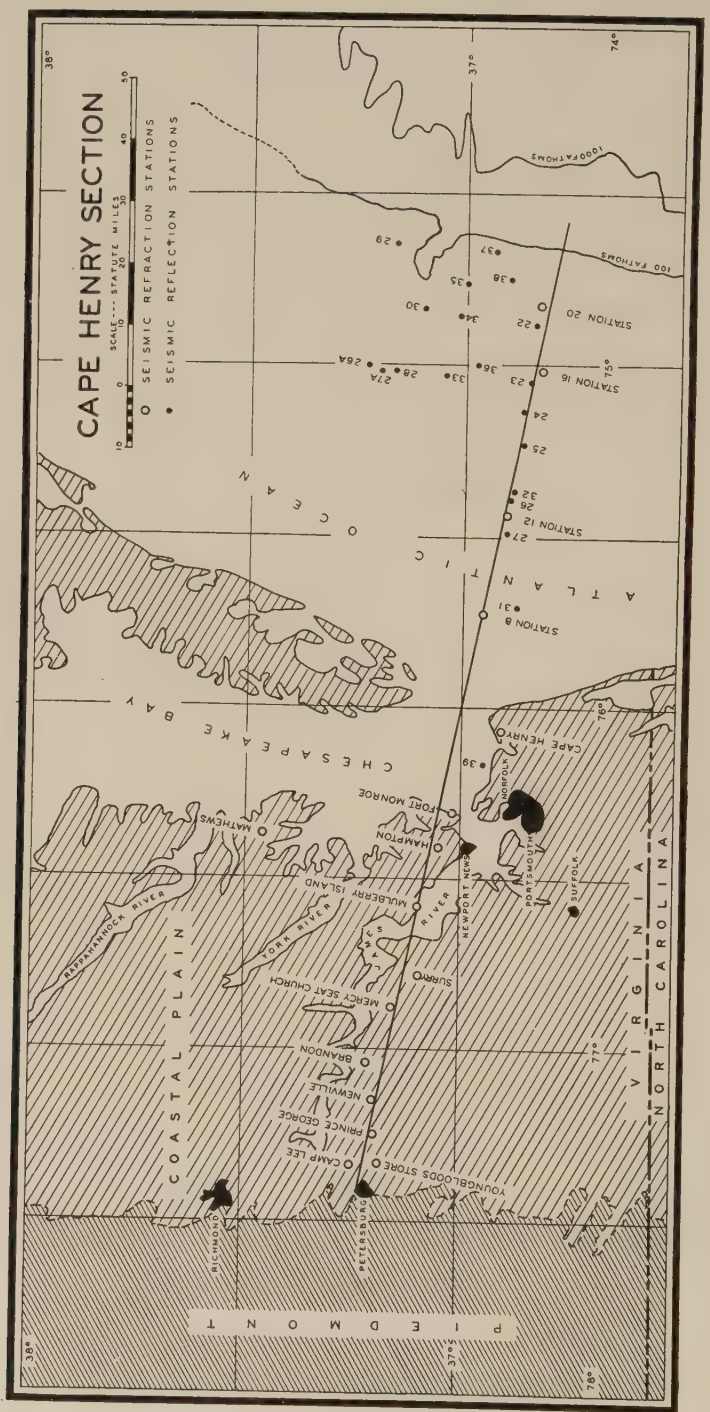


FIGURE 2.—*Map of the Cape Henry section*

passed down the hole and through the charge of dynamite. Shortly before the charge was to be fired, the key of the transmitter was depressed, initiating a signal, which was terminated when the insulated wire was broken by the explosion.

The seismograms were recorded photographically on two three-element, hand-cranked oscillographs (donated by the Geophysical Research Corporation), which were interconnected by a belt to produce an improvised six-element instrument. Each oscillograph contained a 50-cycle tuning fork, which placed time marks on the seismograms at intervals of one hundredth second and served as a standard for measurement of the travel-time. The oscillograph elements had natural frequencies of 90 cycles per second and were approximately critically damped in oil. The geophones used to detect earth vibrations consisted essentially of permanent magnets, mounted on spring suspensions, which permitted motion in the vertical direction only; they were arranged to induce currents in coils attached to the framework. The geophones were adjusted to have natural frequencies of 35 cycles per second and were critically damped in oil. A four-stage resistance-capacity coupled amplifier was used in connection with each of the geophones.

Four geophones, placed at recording points usually spaced at 1000-foot intervals, were used. The radio signal from the shot point, denoting the instant at which the explosion occurred, was recorded photographically in both oscillographs. Where the points were all on a single straight line, distances between shot and recording points were measured by chaining for stations; otherwise, the distances were determined by a transit and stadia rod survey.

At each station, travel-times were measured for several different distances approximately on a straight line, and time-distance graphs were drawn. From these graphs, calculations of velocity and depth were made. Details for individual stations are given in later sections.

METHOD FOR SEA STATIONS

At sea, a blasting gelatin, sometimes used as an oil-well explosive, designed to function effectively under great hydrostatic pressure, was used. The charge was prepared by lashing together the required number of sticks, priming one stick with a waterproof electric blasting cap, weighting the bundle with sash weights, and lowering it to the bottom by means of the firing cable. Ordinarily, these charges were not placed in the water more than 15 minutes before firing. All were prepared, loaded, and fired from a small whale boat, which was at times as far as 8 miles from the ship carrying the recording apparatus. The skill and seamanship of the officers and men of the *Atlantis*, together with remarkably calm weather, which prevailed during the tests, made it possible to obtain

results by this method without taking dangerous chances, but it would be decidedly hazardous to attempt it under less favorable circumstances.

An auxiliary blasting cap, connected in series with the one used as a detonator, served to break a wire in the plate circuit of the transmitter to produce the time-signal. (This cap was placed in air behind a suit-

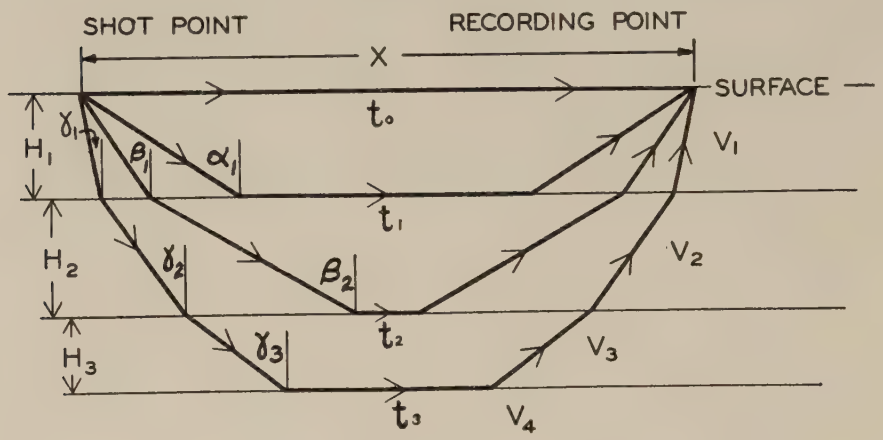


FIGURE 3.—*Paths of seismic waves for refraction method*

able shield, which prevented damage from flying bits of copper.) An excessive current was used to fire the two caps in order to insure against errors in timing, which would be introduced by failure of simultaneous detonation.[4] This arrangement for producing the time signal was selected to avoid the necessity of running wires of the timing circuit to the submerged charge.

Two geophones were used; after the ship was at anchor, they were lowered to the bottom by means of the cables that connected them with the recording apparatus. Suitable bases prevented their overturning. The two geophones were at essentially the same distance from the shot and gave essentially the same data. The use of duplicate geophones and recording systems was definitely worthwhile, because the two records obtained on each shot served to check each other and made simple the problem of distinguishing true ground motions from stray vibrations transmitted down the connecting cables. Where the ship was rolling badly, the geophones were lowered from opposite sides of the vessel, so that one geophone was certain to be undisturbed at any moment, even though the other might be rendered inoperative by a pull on the cable. As an anchored ship usually swings through a considerable arc, it was

[4] G. H. Loving and G. H. Smith: *Explosives and electric blasting caps for geophysical prospecting*, Soc. Petrol. Geophys., Jour., vol. 6 (1935) p. 27.

necessary to organize the work so that the shot could be fired soon after the geophones had reached bottom.

To facilitate the identification of certain waves, one geophone was arranged to give a low-magnification seismogram in addition to the usual high-magnification one. It permitted identification of the wave that travelled through the water. This wave was preceded by one or more waves through the ground. The water wave had a distinctive high-frequency character, which was not present elsewhere on the record. Although the water wave could be readily identified on the low-magnification seismogram, it was considered advisable to remove the possibility of uncertainty in identification by placing a hydrophone a few feet beneath the water and connecting it to record the arrival of the water wave on the seismogram.

The distance for each shot was derived from the travel-time of the water wave, and the general method of measuring the time may be considered comparable to the accurate system of radio acoustic ranging used at present by the United States Coast and Geodetic Survey.[5] Readings of temperature and salinity of the sea water at four depths at each station were taken by A. H. Woodcock, for the purpose of determining the velocity of sound in the water. The results give a mean value of 4949 ± 5 feet per second. A velocity of 4950 feet per second was adopted for calculating all distances. The water wave afforded an accurate and convenient means of measuring the distance.

PRINCIPLES OF INTERPRETATION

The standard method of interpreting the data of the refraction seismograph was used; for convenience, it will be outlined here. Consider the subsurface to be composed of a number of zones, separated from each other by horizontal planes. Let the velocities of seismic waves in the various zones be V_1, V_2, and so on; the thicknesses of the various zones, h_1, h_2, and so on; the travel-times for the various possible paths as shown in Figure 3, t_1, t_2, t_3, and so on. It may be seen that

$$t_1 = x/V_1$$
$$t_2 = 2h_1 \cos \alpha_1/V_1 + x/V_2$$
$$t_3 = 2h_1 \cos \beta_1/V_1 + 2h_2 \cos \beta_2/V_2 + x/V_3$$
$$t_4 = 2h_1 \cos \gamma_1/V_1 + 2h_2 \cos \gamma_2/V_2 + 2h_3 \cos \gamma_3/V_3 + x/V_4$$
$$\sin \alpha_1 = V_1/V_2$$
$$\sin \beta_1 = V_1/V_3, \sin \beta_2 = V_2/V_3$$
$$\sin \gamma_1 = V_1/V_4, \sin \gamma_2 = V_2/V_4, \sin \gamma_3 = V_3/V_4.$$

[5] N. H. Heck, E. A. Eckhardt, M. Keiser: *Radio acoustic method of position finding in hydrographic surveys*, U. S. Coast and Geodetic Surv., Spec. Publ. 107 (1924).

Putting $x = 0$ in these equations and putting T_1, T_2, T_3 for the corresponding values of time, one obtains:

$$T_1 = 2h_1 \cos \alpha_1/V_1$$
$$T_2 = 2h_1 \cos \beta_1/V_1 + 2h_2 \cos \beta_2/V_2$$
$$T_3 = 2h_1 \cos \gamma_1/V_1 + 2h_2 \cos \gamma_2/V_2 + 2h_3 \cos \gamma_3/V_3.$$

These formulas suffice for all calculations on the refraction results made in this report. The travel-time curve represented by these equations consists of several straight lines, or branches, as illustrated in Figure 28. Each path shown in Figure 3 corresponds to a branch of the travel-time curve, and each branch of the curve to a definite subsurface zone. The four zones with which the present paper is concerned will be called the weathered, the unconsolidated, the semi-consolidated, and the crystalline zones. These zones, and also the phases and the branches of travel-time curves associated with them, will be designated by the letters W, U, S, and C, respectively. A phase is a definite arrival of energy as recorded on a seismogram. A phase is said to be normal provided there is some distance at which it will be the first phase to arrive; otherwise, it is said to be masked. For example, the S phase is masked in Figure 24 and is normal in Figure 28. The reciprocal slope of a branch of the travel-time curve gives the velocity of seismic waves in the corresponding subsurface zone. Thus, the values of h_1, h_2, . . . are obtained by substitution in the formulas of the values of V_1, V_2, . . . and T_1, T_2, . . . which are read from the travel-time curves.

Where the boundary plane between two zones is inclined to the surface, a slight modification of the formulas is required; it is also necessary to gather additional data to detect and measure the slope. The method usually used for slopes, known as "reversed profiles", was used on the Surry station and is illustrated in Figure 16. Here, the travel-time to each recording point was measured from two different shot points, one at each end of the line. The travel-times from the two shot points are plotted separately, and a slope in the subsurface layers would be revealed by failure of corresponding branches of the two travel-time curves to show equal velocities. The slope in the surface of the crystallines at the Surry station is seen to be negligible.

A procedure designed to reveal the presence of a slope, without entailing additional observations, was used on most of the land stations. It is well illustrated by the Camp Lee profile (Figs. 4 and 5). The four geophones were placed at stations 1000, 1500, 2000, and 2500 feet along the line of profile. Shots were fired at stations 3000 and 5000, and the eight travel-times obtained from these two shots are plotted on the single curve of Figure 4. The absence of an appreciable slope is shown by the fact that the C branch of the travel-time curve is a single line.

A slope in the surface of the crystalline rocks would cause the four points derived from the shot at 5000 to lie on a line parallèl to, but either above or below, the curve determined by travel-times from the shot at 3000. It should be noted that this method of procedure actually simplified field operations, for the shot point could be moved more

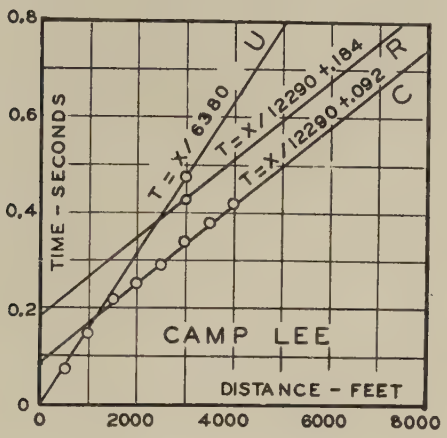


FIGURE 4.—*Travel-time curve for Camp Lee station*

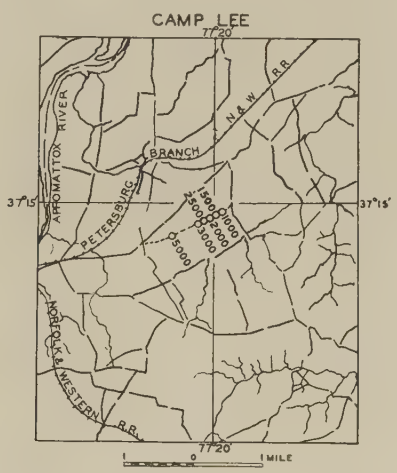


FIGURE 5.—*Station map for Camp Lee*

conveniently than could the geophones, cables, and recording apparatus. At no station was a slope detected.

LATER PHASES

In general, impulses travel from each shot to a recording point along several of the paths sketched in Figure 3. As these impulses usually arrive at different times, each seismogram records several different impulses or phases. "Later phases" are impulses that arrive at the recording point subsequent to the arrival of one, or more, waves. A later phase is recognized on a seismogram by a change in amplitude, frequency, or phase of the recorded motion. Frequently, later phases show only vaguely on seismograms, so that they cannot be identified with the desired degree of certainty. In the present work, certain later phases were so phenomenally distinct that they could be identified positively and timed precisely. Most of the travel-time curves bear many points, which are derived from later phases, especially on the U branches. This favorable circumstance permitted the necessary data to be obtained from a much smaller number of shots than would have been otherwise needed.

On practically every profile the U phase appeared with great amplitude, even at distances so great that two other phases were arriving

ahead of it. From Mulberry Island to Cape Henry the S phase was masked, and appeared only as a later phase. When the data for these four profiles were first obtained, the existence of the S zone had not been

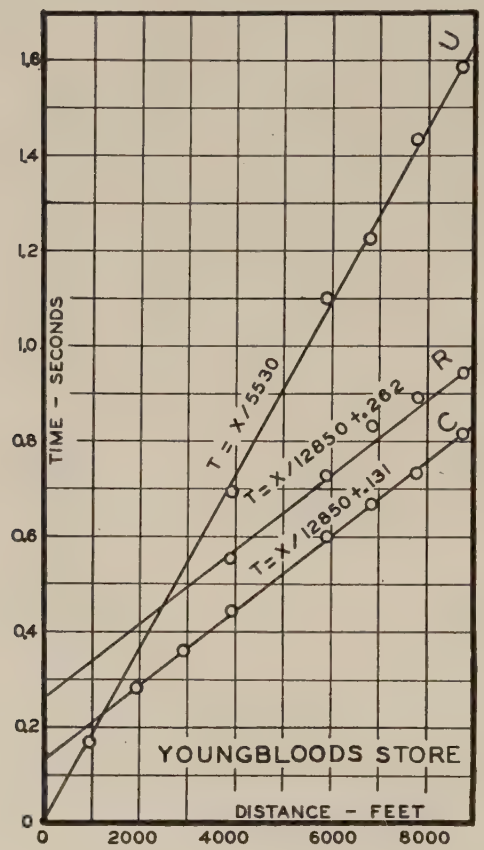


Figure 6.—*Travel-time curve for Youngbloods Store station*

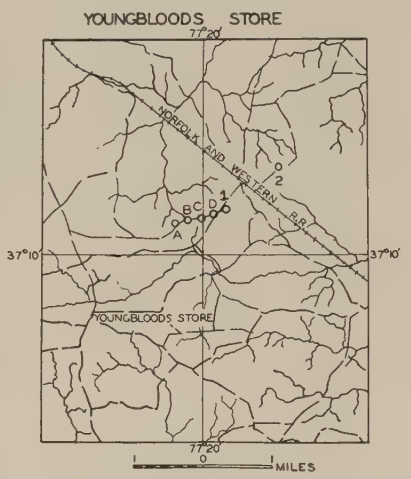


Figure 7.—*Station map for Youngbloods Store*

anticipated. The points for the travel-time curves were plotted as they now appear in Figures 18-24, and those points that are now attributed to the S phase were then very puzzling. Several months later, the data for the adjacent sea stations were obtained. The travel-time curves for stations 8 and 12 reveal the semi-consolidated zone at a depth so slight, compared to that of the crystallines, that the S phase is no longer masked and is the first to arrive over considerable distances. This establishes, beyond question, the existence of the semi-consolidated zone and indicates clearly the proper interpretation for the adjacent land stations.

STATIONS

Camp Lee.—Figures 4 and 5 show the travel-time curve and the sta-

tion map for Camp Lee. This is a good measurement, in which the first arrivals are all sharp and clear. For intermediate distances, the U

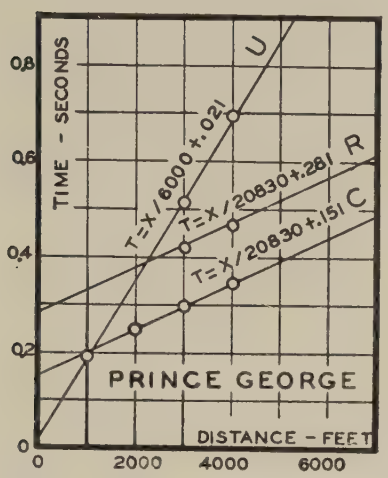


FIGURE 8.—*Travel-time curve for Prince George station*

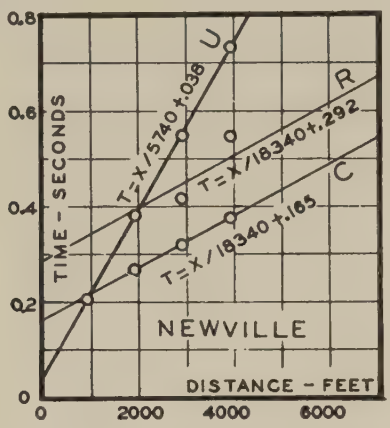


FIGURE 10.—*Travel-time curve for Newville station*

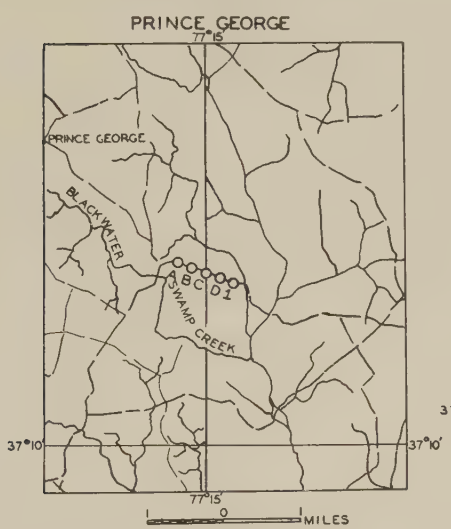


FIGURE 9.—*Station map for Prince George*

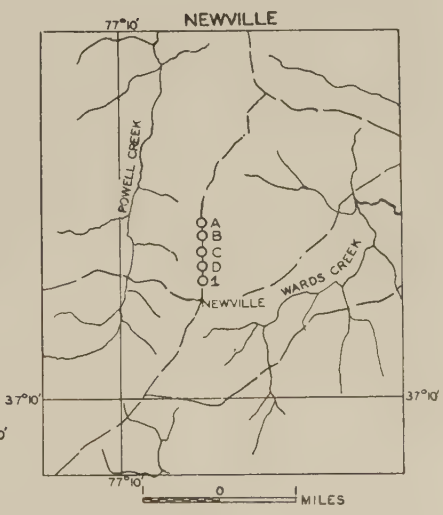


FIGURE 11.—*Station map for Newville*

phase could not be read, because the amplitude of motion on the seismogram was too great. From Figure 31, it is seen that the velocity 12290 ft/sec, obtained here for the crystalline rocks, is far below the normal value.

As is true for all travel-time curves in this report, the lines drawn on the graph and the equations given for these lines were determined by the method of least squares. The travel-time data, calculations, and results for all profiles are given in Tables 2 and 3.

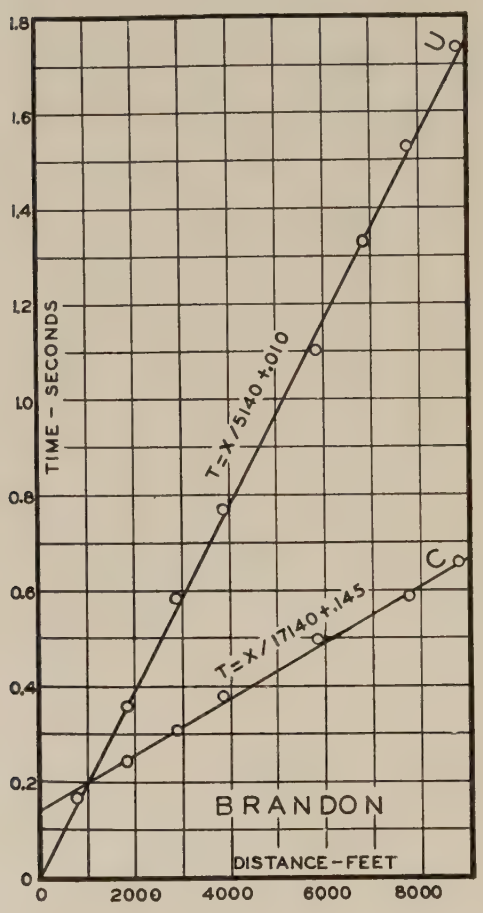


Figure 12.—*Travel-time curve for Brandon station*

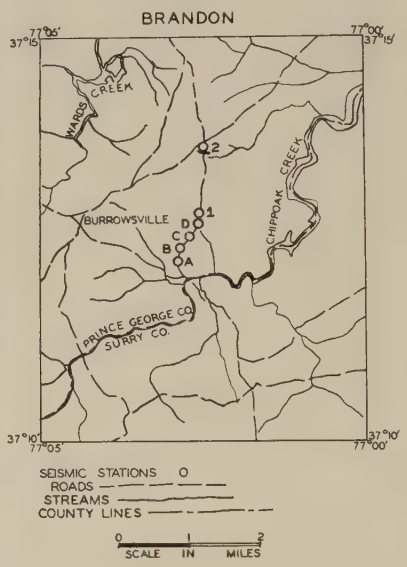


Figure 13.—*Station map for Brandon*

Youngbloods Store.—Figures 6 and 7 show the travel-time curve and the station map for Youngbloods Store. This is a good measurement, having sharp first arrivals and excellent definition of the U branch by later phases. The low velocity of 12850 ft/sec for the crystallines appears here, as at Camp Lee. It is certain that the bedrock here is different than at other places studied in this section. Miller suggests that a buried Triassic Basin may be present beneath these two stations.

A later phase, appearing on the records of this station, is designated as R on the travel-time curve. The line for this phase has the same

slope and double the intercept of the C line. It corresponds to waves that have been reflected once from the surface during their progress from the shot to the recording station. Frequently, it has been considered that

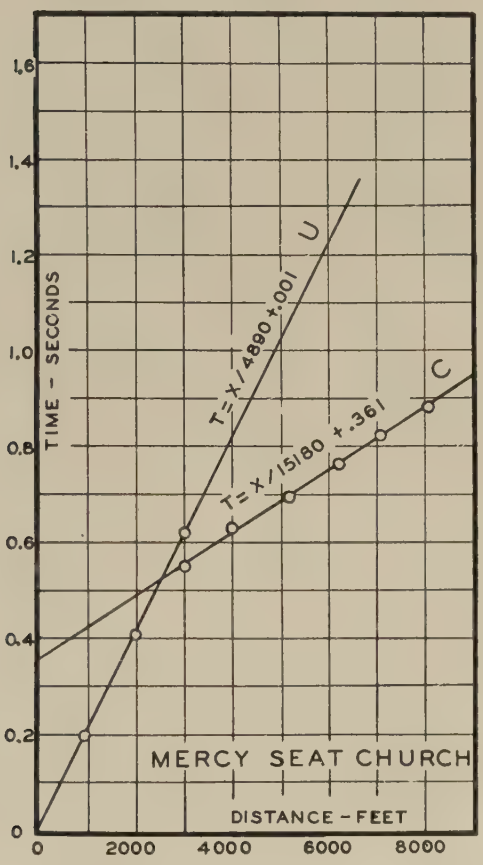


FIGURE 14.—*Travel-time curve for Mercy Seat Church station*

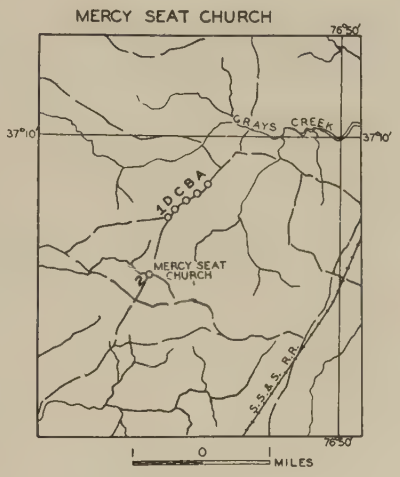


FIGURE 15.—*Station map for Mercy Seat Church*

multiple surface reflections prove that the paths along which the energy travels are curved by refraction, as described by Ewing, in an earlier report,[6] but such is not the case. An interpretation of this reflected phase, on the basis of straight line paths like those of Figure 3, is made, when it is recognized that, although the straight-line system causes the energy reflected at a given surface point to spread out continuously before returning again to the surface, it compensates for this effect by providing a continuous set of points at which the surface reflection may occur. In other words, it is not necessary that the point of reflection of a surface-reflected wave lie midway between the point of

[6] Maurice Ewing and L. D. Leet: *Seismic propagation paths*, Am. Inst. Min. Eng., Tr., Geophys. Prosp. (1932).

origin and the point of reception. Thus, the surface-reflected phase, sometimes considered to be the crucial test, leads to no conclusion whatever in the question of curved paths versus straight ones. The seismograms of this station show fairly good evidence of waves reflected twice at the surface.

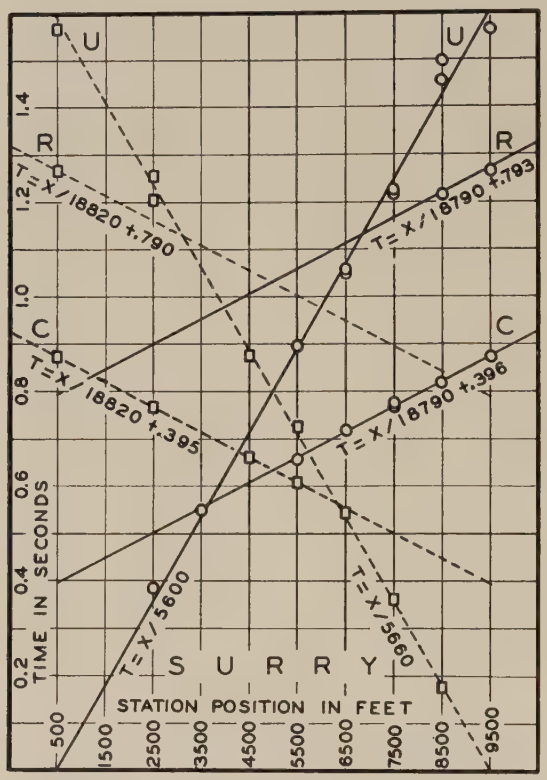


FIGURE 16.—*Travel-time curve for Surry station*

In order to test whether the zone showing the velocity 12580 ft/sec might be underlain at moderate depth by crystalline rocks showing the normal velocity of about 17800 ft/sec, the measurements on this station were extended to a distance of 9000 feet. At this distance the crystalline rocks would have been detected if within 2100 feet of the surface, but no indication of their presence was found.

Prince George.—Figures 8 and 9 show the travel-time curve and the station map for Prince George. This is a good measurement, in which the later phases determine the velocity in the unconsolidated, well enough to permit a depth measurement with only one shot. As only one shot was made, it is impossible to tell whether the observed velocity of 20830 ft/sec represents the true velocity in the crystallines or whether it is altered by a slope in the surface of the crystallines. As no slope was found at any of the stations where the measurements were so arranged that they would have detected it, the most reasonable conclusion is that the observed value of velocity indicates a change in the composition of the rock.

The seismograms of this station clearly exhibit the R phase.

Newville.—Figures 10 and 11 show the travel-time curve and the station map for Newville. In this measurement, the U and C phases are well developed to give a good determination of depth, but no estimation

of slope is possible. The velocity, 18300 ft/sec, obtained here is considered to be the normal value for the crystalline rocks of the entire Cape Henry section.

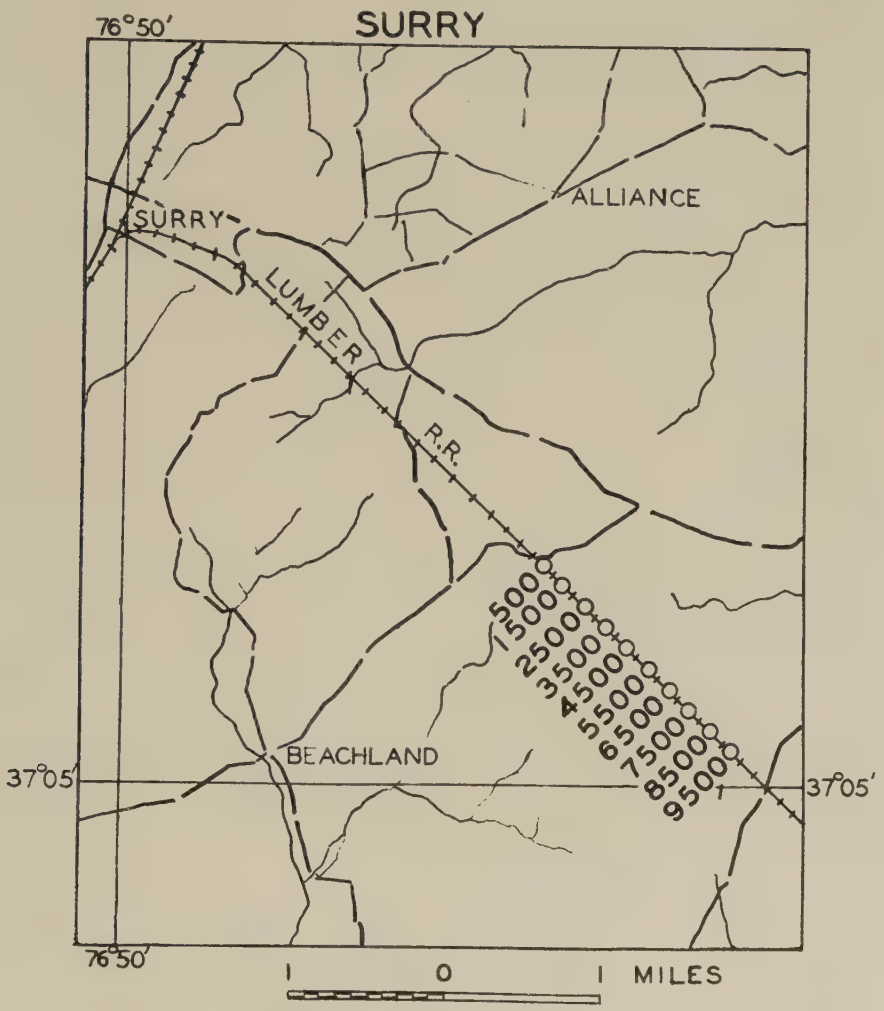


FIGURE 17.—*Station map for Surry*

The R phase looks good on the seismogram, but, as seen from the travel-time curve, the time of arrival of the phase is not in good agreement with the expected value.

Brandon.—Figures 12 and 13 show the travel-time curve and the station map for Brandon. This measurement is satisfactory. The U phase is particularly well developed, and the C phase is acceptable, despite the

fact that on the longer distances the amplitude of earth motion was low enough to impair the precision. No slope is indicated, and the velocity 17100 ft/sec, found for the crystallines, is normal. The R phase could not be identified.

Mercy Seat Church.—Figures 14 and 15 show the travel-time curve and the station map for Mercy Seat Church. The control on depth measurement is excellent, because both the U and the C phases are well developed as first phases. The reflected phase R is probably present, but it cannot be identified with sufficient certainty to justify plotting it on the graph. The U phase is poorly developed at distances where it would appear as a later phase and shows characteristics different from those exhibited at any preceding station. There is slight evidence that the S phase is beginning to appear, but the erratic behavior of U makes definite identification impossible. The travel-time curve indicates that the low velocity observed for C probably was caused by a slight slope.

Surry.—Figures 16 and 17 show the travel-time curves and the station map of Surry. The line of measurement of this station lies along the grade of an abandoned railroad, which runs straight through an unusually level stretch of woods. This station was selected as the one at which to run reversed profiles, in order to test for slope. The velocities for the crystalline from the two profiles agree well enough to indicate zero slope within the limit of accuracy of the measurement.

Phases U, C, and R are well recorded, and the travel-time curves are accurately determined. On two traces the amplifiers were arranged so that only high frequencies (100 cycles, or higher) were recorded, but, even in these cases, both earlier and later phases were readily identified. No evidence of semi-consolidated material could be seen on the excellent records obtained, so it is concluded that semi-consolidated material is not present at Mercy Seat Church.

Mulberry Island.—Figures 18 and 19 show the travel-time curve and the station map for Mulberry Island. This is the most westerly station of the Cape Henry Section that definitely shows the presence of semi-consolidated material. For several months after the data for this station, and for the land stations east of it, were obtained, it seemed impossible to get an interpretation that did not contradict at least one rather well-established fact. When the results from the sea stations became available, the existence of the semi-consolidated zone became obvious. Inclusion of the zone in the calculations for the last four land stations cleared up immediately all difficulties of interpretation.

It should be noted that in the last four land stations the S branch of the travel-time curve is masked—that is, it never appears as a first

arrival. This circumstance is due to the presence of the crystalline zone, in which the velocity is high, at a depth not sufficiently in excess of that of the semi-consolidated material to prevent masking by the waves through the crystalline zone. The masking disappears for the sea sta-

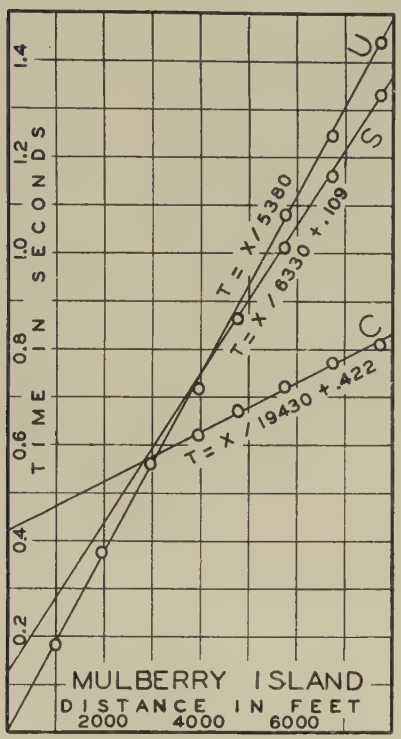


FIGURE 18.—*Travel-time curve for Mulberry Island station*

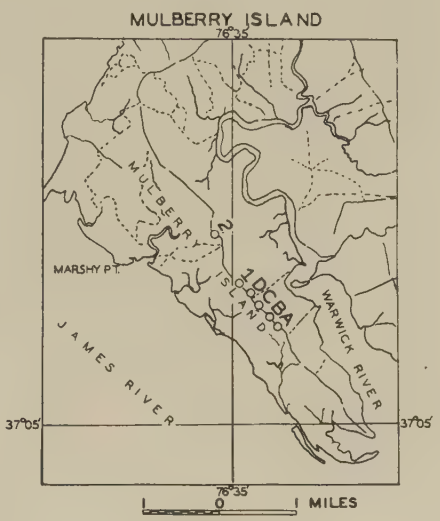


FIGURE 19.—*Station map for Mulberry Island*

tions, simply because the thickness of the semi-consolidated material is greater at those stations. Allen [7] has discussed a similar situation. With reference to some travel-time curves, which he has worked out for a hypothetical structure, he states:

"It is apparent that the wave from the third horizon would never be the first impulse, since the intersection of the T_2 and T_3 curves is past the point where the T_4 wave arrives first. The only manner by which the third horizon velocity may be determined is to select the secondary waves on records shorter than 4.174 kilometers, which is the value of x where the T_2 and T_4 curves intersect in this particular case."

Allen fails to mention the possibility that his "masked" T_3 waves may be picked as second arrivals beyond the point where they cross the T_2 line—the most likely of the two possibilities, except in cases further complicated by abnormal absorption of elastic energy. At any rate, the

[7] T. L. Allen: *Use of record character in interpreting results and its effect on depth calculation in refraction work*, Am. Assoc. Petrol. Geol., Bull., vol. 16 (1932) p. 1212.

phases used in the present work to map the masked horizon are quite definite and give a satisfactory solution to the problem.

The velocity found here for the crystalline is considered to be normal and not appreciably influenced by slope.

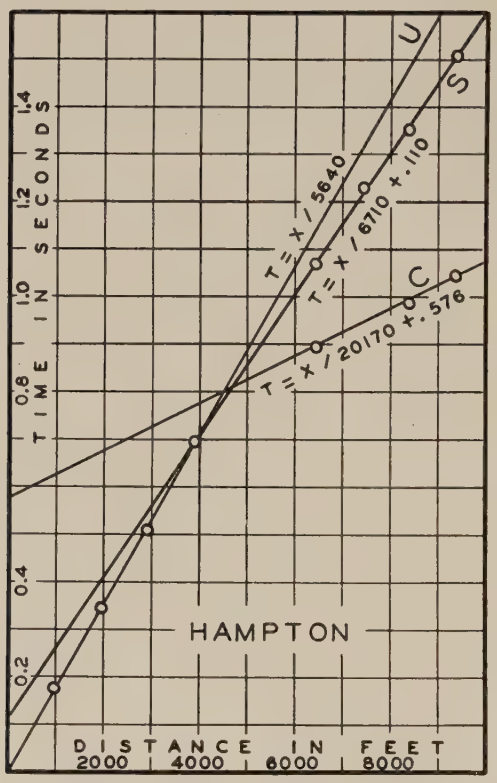


FIGURE 20.—*Travel-time curve for Hampton station*

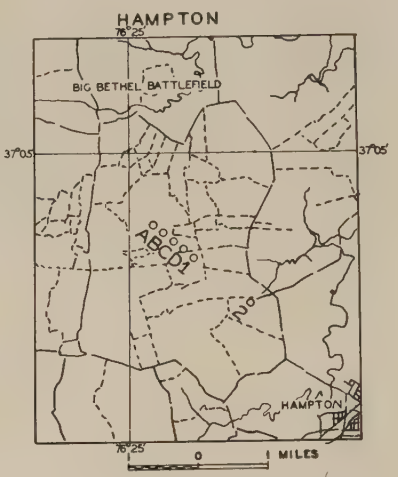
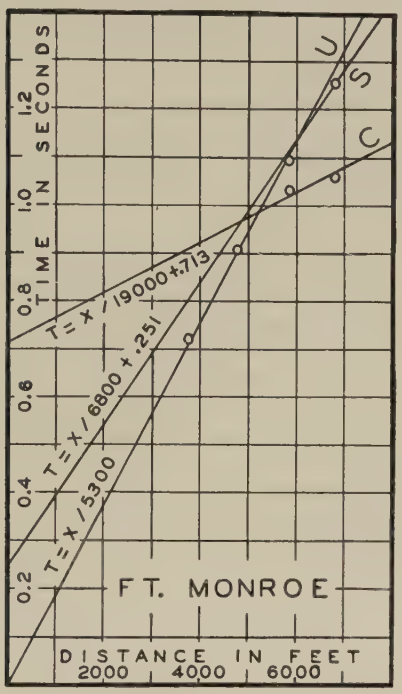


FIGURE 21.—*Station map for Hampton*

Hampton.—Figures 20 and 21 show the travel-time curve and the station map for Hampton. The measurements for this station followed a line of the Chesapeake and Potomac Telephone Company, through a dense wood, and the writers are indebted to E. G. Magruder, of that company, for assistance in locating the station on the map. The seismic data are satisfactory but are not exceptionally precise. All three branches of the travel-time curve are well determined, but it was impossible to pick out the waves through the unconsolidated zone as third arrivals at the greater distances. The presence of the semi-consolidated zone is clearly shown.

Fort Monroe.—Figures 22 and 23 show the travel-time curve and the station map for Fort Monroe. This is a poor measurement. Ground

unrest, caused by running machinery and traffic, difficulty in sinking a hole of suitable depth for burying the charge of explosive, and other hindrances imposed by the geography of the location made it impossible to get seismograms which could be read with high accuracy. Further, only



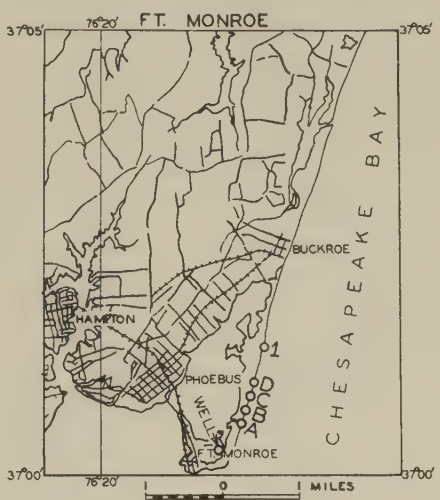


FIGURE 23.—*Station map for Fort Monroe*

FIGURE 22.—*Travel-time curve for Fort Monroe station*

one shot was made, and the data are, therefore, meager and do not suffice to give velocities in the semi-consolidated and crystalline zones at this point. For calculating the depths, the velocities for the semi-consolidated and the crystalline zones were taken as 6800 ft/sec and 19000 ft/sec, respectively, by interpolation between the values found for adjacent stations. From the composite velocity diagram of Figure 31, it may be seen that the interpolation is valid. Although the data available at this station would not be adequate for a satisfactory depth determination if the station stood alone, a reliable calculation becomes possible when the interpolations are made. The depth to the crystalline rocks, calculated from the seismic measurements, is 2260 feet. The depth to crystalline rocks found in the deep well drilled inside Fort Monroe in 1902 is 2243 feet.[8] The agreement is perhaps partly fortuitous, and the error less than the probable error of the seismic determination, in view of the poor quality

[8] Samuel Sanford: *Underground water resources of the coastal plain province of Virginia*, Va. Geol. Surv., vol. 5 (1913) p. 99.

of the data available. There would be a large discrepancy between seismic result and well log, if the S phase, which is masked here, had been

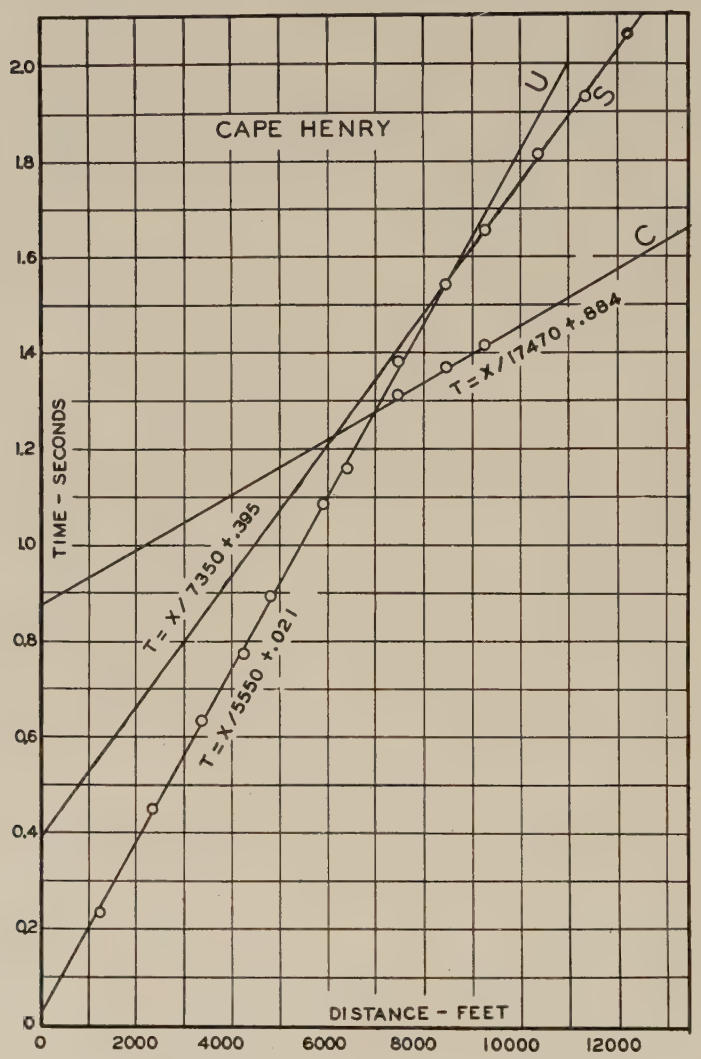


FIGURE 24.—*Travel-time curve for Cape Henry station*

overlooked. The well is located almost a mile south of the center of the line on which the seismic measurements were made (Fig. 23).

Cape Henry.—Figures 24 and 25 show the travel-time curve and the station map for Cape Henry. The branches of the travel-time curve for

the unconsolidated and semi-consolidated zones are well determined. The branch for the crystalline is determined with only moderate accuracy,

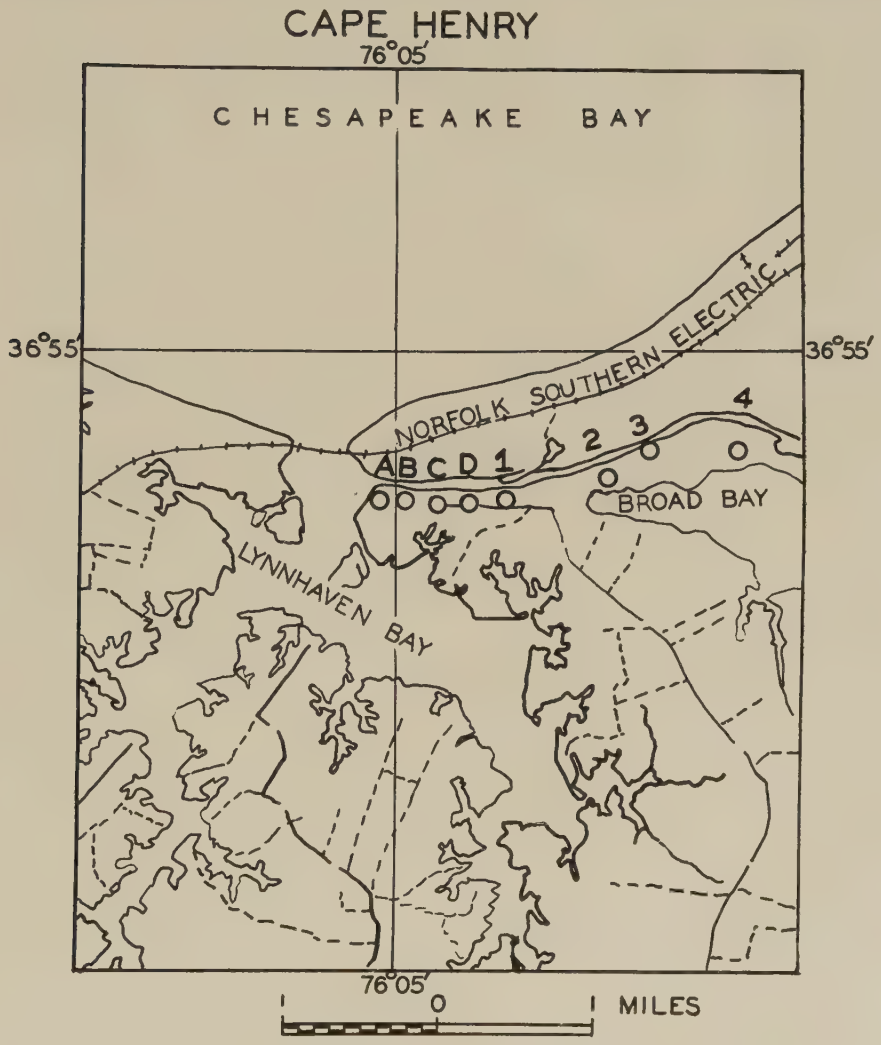


FIGURE 25.—*Station map for Cape Henry*

because the first arrivals on the seismograms at the greater distances were low in amplitude. It was not feasible to get more amplitude, because the explosive charges could not be buried deeply enough for effective performance in the sand dune terrain of this locality. With the hand augers used for sinking the shot holes, it was impossible to go beneath the water table.

Even though the shot points were on the highest sand dunes available, the 12 or 15 feet of loose sand lying above the shot did not provide sufficient confinement.

This measurement is reliable and gives an ideal example of the application of the refraction seismograph to places where one zone is masked by the presence of an underlying zone of much higher velocity.

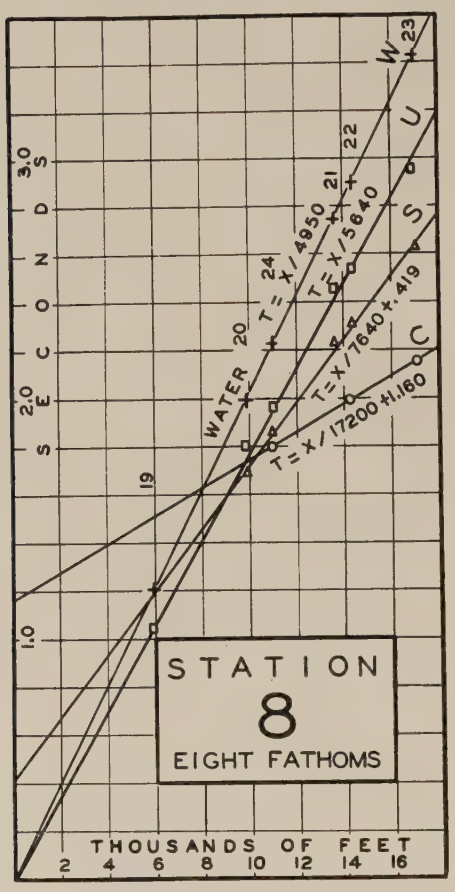


FIGURE 26.—*Travel-time curve for Station 8*

No. 8.—Figures 26 and 27 show the travel-time curve for Station 8 and the station maps for all sea stations. The measurement at Station 8 is quite satisfactory. Each branch of the travel-time curve is well determined, and the velocities and depths obtained are consistent with those found at Cape Henry, the adjacent land station. This is the first station described in this report for which the wave through the semi-consolidated zone is not masked.

On the record of Shot 20, there is a feeble phase at 1.609 seconds, which has not been plotted on the graph. It is likely that this phase is a "leader", similar to those which will be described under the discussion of the measurements at Matthews.

No. 12.—Figure 28 shows the travel-time curve for Station 12. This is the best of the sea stations. The U phase is picked on the low-magnification record. It is an angular impulse, larger in amplitude than any arriving before it, which may be correlated from shot to shot with certainty. Study of the high-magnification records shows that this phase might be picked a trifle earlier, but the low-magnification readings are accepted because of the definite nature of the correlation which may be made from them. No essential variation in interpretation is involved.

The S phase is characterized by a gradual building up to a regular sinusoidal wave of rather low frequency. It is readily identifiable by its character. This phase is unaccountably almost 0.2 second early on Shot 31.

The C phase is of low amplitude on the three longest shots, but it is definite. The first phase of Shot 29 is intentionally used for both the C and the S branches of the curve, on the basis of record character.

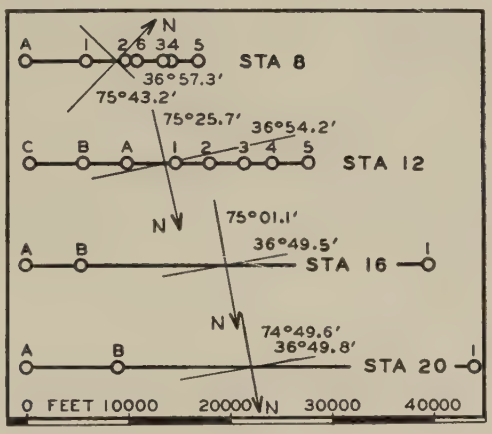


FIGURE 27.—*Station map for Stations 8, 12, 16, and 20*

No. 16.—Figure 29 shows the travel-time curve for Station 16. This determination is incomplete, because both the number of shots and the amount of explosive used on each shot had to be curtailed because of a shortage of the dynamite supply. It is decidedly unfortunate that more data could not have been obtained here, because a few shorter shots would be of great value in determining the S phase more accurately.

The U phase may be considered to be completely determined by the data at hand. The value obtained is consistent with those for preceding stations.

The velocity for S was taken, by extrapolation from Figure 31, as 8180 ft/sec, and a line of this slope was drawn between the two points available for fixing the position of this branch of the curve. Because of the poor control of the S branch, the depth given for the semi-consolidated zone must be considered no better than a rough approximation.

No direct evidence, whatever, was obtained for the depth to the crystalline zone, so nothing more than a minimum limit for the depth to it can be set. The velocity of 18000 ft/sec for C was taken by extrapolation from Figure 31. The record for Shot 32 is poor, so that one may not be certain whether or not a C phase arrived ahead of the S. A good record was obtained from Shot 33, and it is certain that no phase arrived ahead of the one plotted. Therefore, the depth given for the crystalline zone is not an observed depth but, rather, the minimum depth that is consistent with the observed data.

No. 20.—Figure 30 shows the travel-time curve for Station 20. The data here are more complete than at Station 16 but are still decidedly

inadequate, because of the shortage of the explosive supply. The U phase is satisfactory. The velocity 8390 ft/sec for S, obtained by linear extra-

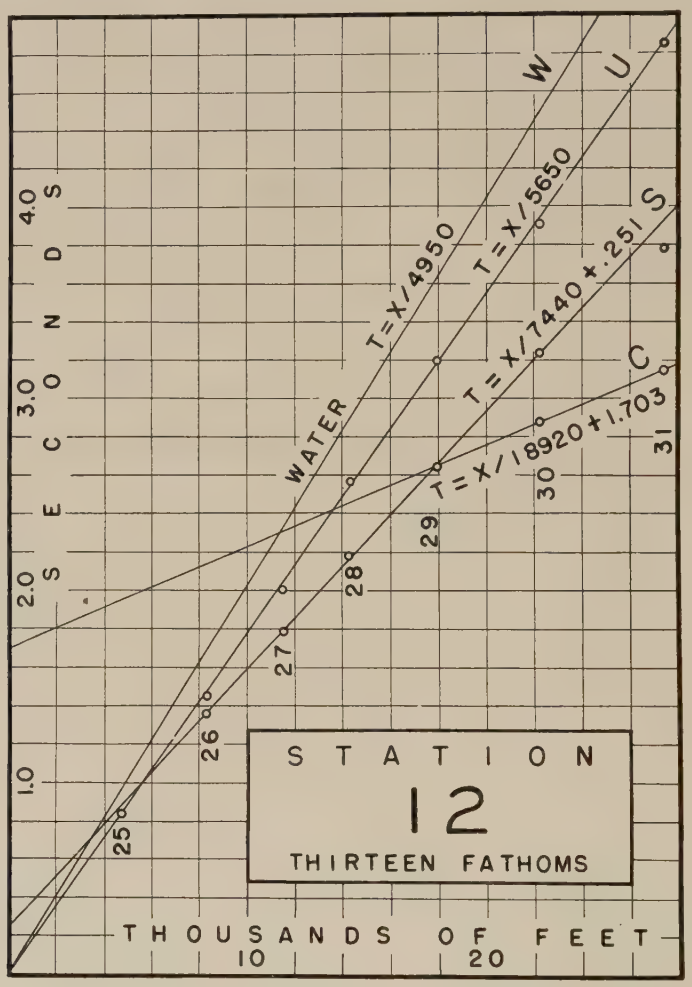


FIGURE 28.—*Travel-time curve for Station 12*

polation from Figure 31, is in good agreement with the two points available on the travel-time curve, but these points afford poor control on the calculation of the depth to the semi-consolidated zone. The velocity 18000 ft/sec for the C phase is, likewise, obtained by extrapolation, but the point on the travel-time curve through which the C line is drawn is quite definite on the seismogram. The depth to the crystalline zone obtained here is, therefore, reliable insofar as the basic assumption—that the three

zones revealed by the stations to the west persist here—is justified, for which there is considerable evidence from the seismograms.

For Shot 35, the geophones were on the bottom, in 46 fathoms; they functioned perfectly at that depth. The depth of 35 fathoms given on Figure 30 refers to the average depth over the 8-mile line covered by the measurements for this station.

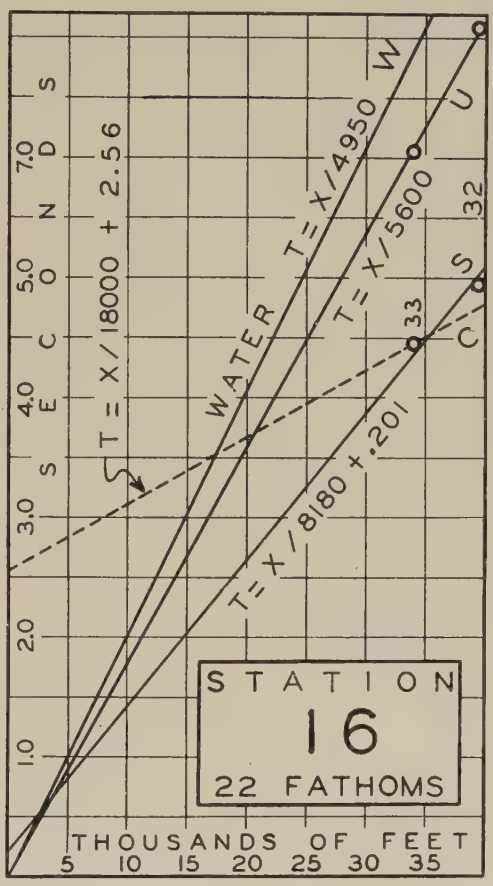


FIGURE 29.—*Travel-time curve for Station 16*

VELOCITY ANALYSIS

Figure 31 shows the velocities found for the three zones, for the entire Cape Henry section. All values obtained by interpolation are enclosed in dotted circles.

The velocity for U remains reasonably constant and has no uniform trend. The curve for S shows a uniform trend, the velocity increasing to the east. The straight line shown through these points was used as the basis for the interpolation. Toward the west, the velocity for S becomes so low that it is difficult to distinguish this phase from U. This accounts for S being terminated rather abruptly at the Mulberry Island Station (Fig. 32).

The velocities of C fluctuate considerably, probably because of the effects of slopes, which were not completely eliminated by the method of controlling slope used in the work. The only variation of velocity to which significance is attached is that found at Camp Lee and at Youngbloods Store, which has been mentioned as indicating a Triassic basin.

RECORD CHARACTER

As a rule, those phases on seismograms that represent refracted waves have gradual beginnings. Even though large charges of explosives are

used, it is often difficult to cause refracted waves to begin sharply enough for satisfactory timing. Contrary to this rule, all waves refracted through the crystalline rocks at land stations in the present work show sharp beginnings, having a characteristic wave-shape resembling the letter W. Following the large amplitude beginnings, there is little motion on the record until the S and the U phases arrive. The C phases were so small at the sea stations that it cannot be stated with certainty that they possess the characteristic shape.

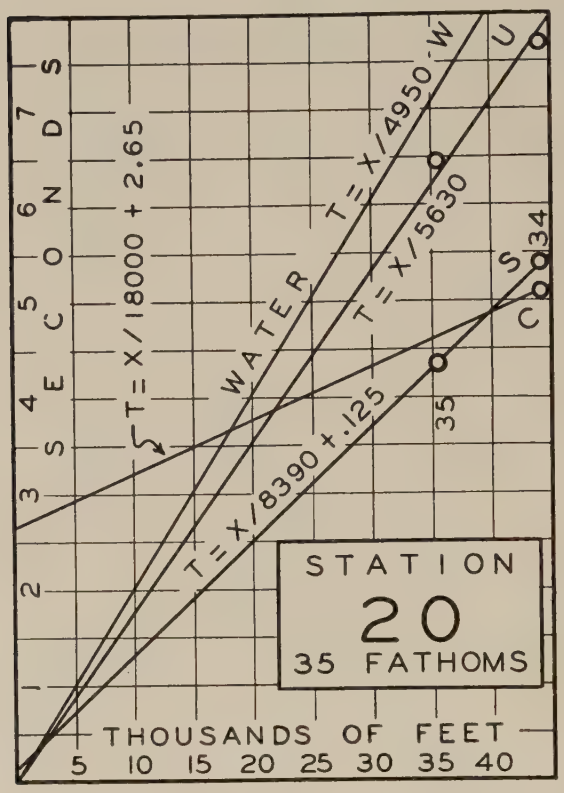


FIGURE 30.—*Travel-time curve for Station 20*

Records from land stations show prominent "ground roll". This consists of a long train of waves—period 0.06 to 0.13 second, velocity 800 to 2000 ft/sec, amplitude large—that are usually considered to be similar to the Rayleigh waves and the Love waves observed in the seismograms of earthquakes. These waves are completely absent at sea stations, and this feature is the outstanding point of difference between the two sets of records. Even in the earlier portions of the seismograms, the frequencies of the waves at sea stations are higher—roughly twice as high—than those for land stations. Plate 1 shows tracings of some refraction seismograms, which illustrate some of these features.

SUMMARY

Table 2 shows a summary of all the travel-time data for the stations of this section. For the sea stations of this section, the distances were obtained by multiplying the travel-time of the water wave, indicated by w in Table 2, by 4950 ft/sec. The shot locations and recording locations are on the station maps.

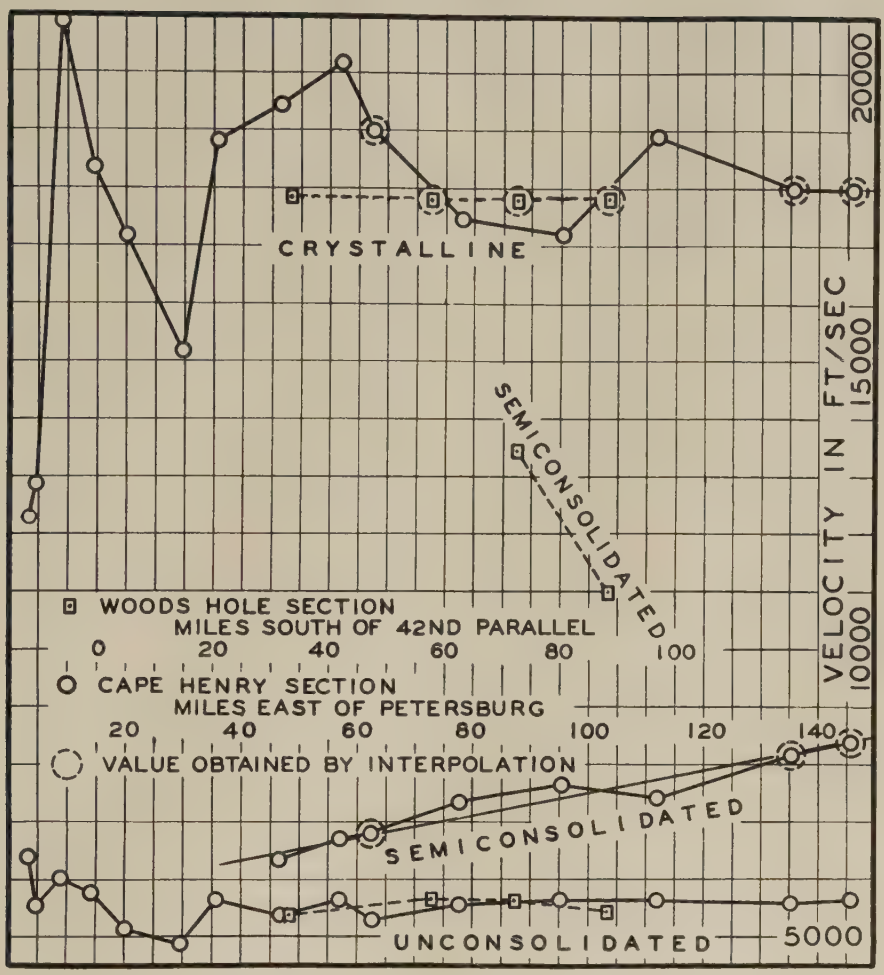


FIGURE 31.—*Velocity chart for Cape Henry and Woods Hole sections*

Table 3 summarizes the calculations and results. All values of velocity and time shown in this table were taken from the various travel-time curves. The values of h refer to the thicknesses of the various zones and were calculated by means of the formulas given on p. 763. The elevations given in the last three columns are taken with reference to sea level and refer to the upper surfaces of the zones for which they are given.

Figure 32 shows the section across the coastal plain, which has been constructed from the seismic measurements already described. The uniform elevation of the surface of the crystalline zone at the five most westerly stations should be noted. Possibly, the change from this uniform elevation is more abrupt than is shown in the section. It should be re-

TABLE 2.—*Time distance data for all refraction stations*

Shot number	Charge of explosive (lb.)	Shot hole depth (ft.)	Shot location	Recording location	Distance X (ft.)	Travel Time U (sec.)	Travel Time S (sec.)	Travel Time C (sec.)	Travel Time R (sec.)
Camp Lee, August 14, 1935									
1	3.5	15	3000	2500	500	0.071	.....	.....	.....
8/14				2000	1000	0.148	.....	.....	.....
				1500	1500	os	.....	0.218	.....
				1000	2000	os	.....	0.252	.....
2	6.0	20	5000	2500	2500	os	.....	0.290	.....
8/14				2000	3000	0.474	.....	0.338	0.429
				1500	3500	os	.....	0.378	os*
				1000	4000	os	.....	0.417	os
Youngbloods store, August 17, 1935									
1	3.5	10	1	D	1000	0.169	.....	.....	.....
8/17				C	1985	os	.....	0.283	.....
				B	2976	os	.....	0.360	.....
				A	3970	0.694	.....	0.444	0.558
2	10.0	17	2	D	5956	1.099	.....	0.600	0.730
8/17				C	6896	1.225	.....	0.670	0.833
				B	7833	1.433	.....	0.733	0.892
				A	8784	1.585	.....	0.815	0.947
Prince George, August 16, 1935									
2	3.5	10	1	D	1000	0.192	.....	.....	.....
8/16				C	2000	0.352	.....	0.247	.....
				B	3000	0.513	.....	0.295	0.419
				A	4000	0.694	.....	0.343	0.466
Newville, August 16, 1935									
1	3.5	12	1	D	1000	0.214	.....	.....	.....
8/16				C	2000	0.388	.....	0.275	.....
				B	3000	0.554	.....	0.328	0.425
				A	4000	0.730	.....	0.384	0.559
Brandon, August 15, 1935									
2	.....	.....	1	D	767	0.167	.....	.....	
8/15				C	1813	0.355	.....	0.249	
				B	2868	0.582	.....	0.305	
				A	3871	0.769	.....	0.379	
1	6.0	17	2	D	5821	1.100	.....	0.496	Low
8/15				C	6797	1.336	.....	.....	ampli-
				B	7757	1.525	.....	0.587	tude
				A	8786	1.731	.....	0.658	
Mercy Seat Church, August 18, 1935									
1	.....	.....	1	D	965	0.202	.....	.....	.....
8/18				C	2052	0.413	.....	.....	.....
				B	3045	0.627	.....	0.556	.....
				A	4055	poor	.....	0.636	.....
2	.....	.....	2	D	5232	.....	.....	0.702	.....
8/18				C	6247	poorly	.....	0.774	poorly
				B	7133	devel-	.....	0.831	devel-
				A	8101	oped	.....	0.892	oped

* Off-scale on the seismogram.

TABLE 2.—*Time distance data for all refraction stations—continued*

Shot number	Charge of explosive (lb.)	Shot hole depth (ft.)	Shot location	Recording location	Distance X (ft.)	Travel Time			
						U (sec.)	S (sec.)	C (sec.)	R (sec.)
Surry, August 12–13, 1935									
1	5.5	10	500	1500	1000	.....	.....	.....	.....
8/12				2500	2000	0.384	.....	.....	.....
				3500	3000	0.551	.....	.....	.....
				4500	4000	.....	.....	.....	.....
4	.....	.....	500	5500	5000	0.896	.....	0.659	.....
8/12				6500	6000	1.059	.....	0.719	.....
				7500	7000	1.226	.....	0.767	.....
				8500	8000	1.454	.....	0.816	1.218
1	.....	.....	500	6500	6000	1.052	.....	0.716	.....
8/13				7500	7000	1.220	.....	0.773	.....
				8500	8000	1.498	.....	0.828	.....
				9500	9000	1.564	.....	0.874	1.268
3	.....	.....	9500	8500	1000	0.177	.....	.....	.....
8/12				7500	2000	0.361	.....	.....	.....
				6500	3000	0.543	.....	.....	.....
				5500	4000	0.725	.....	0.608	.....
2	.....	.....	9500	4500	5000	0.877	.....	0.661	.....
8/12				3500	6000	.....	.....	.....	.....
				2500	7000	1.257	.....	0.766	1.203
				1500	8000	.....	.....	.....	.....
				(500)	9000	1.564	.....	0.874	1.268
Mulberry Island, August 19–20, 1935									
1	.....	.....	1	D	1000	0.183	.....	.....	.....
8/20				C	1985	0.387	.....	.....	.....
				B	2980	0.561	.....	.....	.....
				A	3979	0.718	.....	0.621	.....
2	.....	.....	2	D	4780	.....	0.866	0.672	.....
8/20				C	5758	1.082	1.012	0.723	.....
				B	6731	1.244	1.165	0.774	.....
				A	7725	1.440	1.331	0.812	.....
Hampton, August 3–5, 1935									
1	4.0	15	1	D	975	0.177	.....	.....	.....
8/3				C	1950	0.343	.....	.....	.....
				B	2925	0.510	.....	.....	.....
				A	3900	0.697	.....	.....	.....
1	9.0	.....	2	D	6442	.....	1.065	0.897	.....
8/5				C	7417	.....	1.228	.....	.....
				B	8392	.....	1.350	0.988	.....
				A	9367	.....	1.507	1.043	.....
Fort Monroe, August 21, 1935									
1	.....	10	1	D	3766	0.721	.....	.....	.....
8/21		bay		C	4789	0.909	.....	.....	.....
				B	5848	1.095	.....	1.033	.....
				A	6811	.....	1.253	1.060	.....

TABLE 2.—*Time distance data for all refraction stations—continued*

Shot number	Charge of explosive (lb.)	Shot hole depth (ft.)	Shot location	Recording location	Distance X (ft.)	Travel Time			
						U (sec.)	S (sec.)	C (sec.)	W (sec.)
Cape Henry, August 6–7, 1935									
1			1	D	1222	0.235	.....	.....	.....
8/6				C	2332	0.449	.....	.....	.....
				B	3357	0.634	.....	.....	.....
				A	4253	0.772	.....	.....	.....
2			2	D	4803	0.893	.....	.....	.....
8/6				C	5899	1.085	.....	.....	.....
1	16.5		3	D	6397	1.159	.....	.....	.....
8/7				C	7476	1.379	.....	1.311	.....
				B	8446	1.539	.....	1.370	.....
2			4	D	9256	.....	1.654	1.413	.....
8/7				C	10360	.....	1.811	.....	.....
				B	11350	.....	1.931	.....	.....
				A	12220	.....	2.062	.....	.....
Station 8, October 26, 1935									
19	1.5	.....	1	A	5960	1.046	.....	.....	1.205
20	2	.....	2	A	9860	1.799	1.696	.....	1.993
21	5	.....	3	A	13600	2.454	2.224	.....	2.748
22	5	.....	4	A	14340	2.539	2.309	1.993	2.898
23	15	.....	5	A	17010	2.950	2.624	2.148	3.436
24	10	.....	6	A	11020	1.956	1.862	1.800	2.226
Station 12, October 27, 1935									
25	2	.....	1	A	4780	0.840	.....	.....	0.966
26	3	.....	2	A	8250	1.455	1.361	.....	1.666
27	5	.....	3	A	11530	2.008	1.793	.....	2.329
28	6	.....	4	A	14350	2.570	2.199	.....	2.899
29	8	.....	5	A	17920	3.215	2.650	2.650	3.620
30	15	.....	5	B	22240	3.906	3.245	2.879	4.494
31	20	.....	5	C	27440	4.852	.....	3.153	5.543
Station 16, October 28, 1935									
32	20	.....	1	A	39520	7.09	4.95	.....	7.983
33	30	.....	1	B	34080	6.06	4.45	.....	6.884
Station 20, October 28, 1935									
34	25	.....	1	A	44030	7.68	5.39	5.10	8.894
35	25	.....	1	B	35500	6.46	4.34	.....	7.172
Woods Hole, October 16, 19, 1935									
2		.....	4	B	3520	.....	.....	.286	.711
3		.....	5	B	1980	.....	.....	.185	.400
16		.....	1	A	1170	.231	.....	.154	.....
		.....	1	B	570	.110	.....	.....	.....
17		.....	2	A	2560	.....	.....	.228	.518
		.....	2	B	1940	.....	.....	.194	.391
18	3	.....	3	A	4140	.....	.....	.307	.836
		.....	3	B	3590	.665	.....	.291	.725
Station 1, October 17, 1935									
5		.....	3	A	2260	.408	.....	.....	.456
		.....	3	A′	2360	.433	.....	.....	.476
6		.....	2	A	3300	.581	.....	.....	.667
7	2	.....	1	A	4360	.756	.....	.655	.881
Station 3, October 18, 1935									
13	5	.....	1	A	11090	1.932	1.343	.....	2.241
14	6	.....	2	A	9460	1.763	.....	.....	1.911
15	6	.....	2′	A	9260	1.589	1.207	.....	1.871

TABLE 2.—*Time distance data for all refraction stations—continued*

Shot number	Charge of explosive (lb.)	Shot hole depth (ft.)	Shot location	Recording location	Distance X (ft.)	Travel Time			
						U (sec.)	S (sec.)	C (sec.)	W (sec.)
Station 2, October 18, 1935									
9	2	.....	1	A	2540	.450	.....	.....	.514
10	4	.....	2	A	4920	.917	.....	.....	.991
11	4	.....	3	A	7060	1.290	1.192	.....	1.426
12	6	.....	4	A	8600	1.583	1.332	.....	1.738
Mathews, July 28–31, 1935									SH
2		18	1	9	534	.....	.....	.....	.088
7/31				7	1112	.207	.....	.....	.146
				5	1655	.316	.....	.....	.260
				4a	2021	.386	.....	.....	.347
1	6.5	18	1	4a	2021	.386	.....	.....	.352
7/31				1	2975	.576	.....	.....	.....
				15	3993	.787	.....	.....	.....
				17a	4925	.986	.....	.929	.....
1	8.5	18	1	4000	5737	1.133	.....	.962	.....
7/30				3000	6706	.....	1.238	1.012	.....
				2000	7686	.....	1.385	1.063	.....
				1000	8664	.....	.....	1.114	.....
1	.....	18	1	4000	5737	1.125	.....	.963	.....
7/29				3250	6498	1.264	.....	.987	.....
				2750	7018	.....	1.250	1.030	.....
				2000	7686	.....	1.382	1.067	.....
1	6.5	18	1	2000	7686	.....	1.341	1.057	.....
7/28				1000	8664	.....	1.486	1.119	.....
				0	9650	.....	1.635	1.157	.....

membered that the results given for the two most easterly stations are based on meager data and on the assumption that the velocities are roughly the same as at neighboring stations.

REFRACTION MEASUREMENTS ON THE WOODS HOLE SECTION

LOCATION

The Woods Hole section lies along the meridian 70°43′ West. The position of the stations along this line are measured in statute miles south of the 42nd Parallel. Four stations were occupied for these, the first refraction, measurements made at sea. The primary purpose of these measurements was to develop the technique and to make certain that the instruments were working properly before getting too far away from the base at Woods Hole, Massachusetts. Although the results are incomplete, they offer enough substantiation to those obtained at Cape Henry to justify inclusion here.

TABLE 3.—*Calculations and results for refraction measurements*

Station	V_W ft./sec.	V_U ft./sec.	T_U sec.	h_W ft.	V_S ft./sec.	T_S sec.	h_U ft.	V_C ft./sec.	T_C sec.	h_S ft.	Elev. Surf. ft.	Elev. semicon. ft.	Elev. cryst. ft.
Camp Lee	.....	6381	.....	0	.....	.....	342.6	12290	.0918	0	+110	.....	− 230
Youngbloods store	.....	5532	.....	0	.....	.....	401.0	12850	.1309	0	+140	.....	− 260
Prince George	2000*	5999	.0210	22.3	.....	.....	403.5	20830	.1510	0	+130	.....	− 300
Newville	2000*	5741	.0383	40.9	.....	.....	377.0	18340	.1655	0	+120	.....	− 300
Brandon	2000*	5145	.0101	11.0	.....	.....	361.0	17140	.1450	0	+ 70	.....	− 300
Mercy Seat Church	2000*	4894	.0010	1.1	.....	.....	929	15180	.3607	0	+100	.....	− 830
Surry 500	.....	5605	.....	0	.....	.....	1164	18790	.3965	0	+ 90	.....	−1070
Surry 9500	.....	5660	.....	0	.....	.....	1152	18820	.3951	0	+ 90	.....	−1060
Mulberry Island	.....	5376	.....	0	6331	.1086	553	19430	.4223	752	+ 10	− 540	−1300
Hampton	.....	5645	.....	0	6714	.1102	575	20170	.5761	1353	+ 10	− 570	−1920
Fort Monroe	.....	5296	.....	0	6800*	.251	1060	19000*	.713	1198	0	−1060	−2260
Cape Henry	2000*	5551	.0207	22.2	7347	.3949	1582	17470	.8841	1303	+ 10	−1590	−2900
Station 8	.....	5644	.....	0	7640	.4194	1756	17200	1.160	2439	− 50	−1810	−4250
Station 12	.....	5650	.....	0	7435	.2513	1092	18920	1.703	5410	− 80	−1170	−6580
Station 16	.....	5595	.....	0	8180*	.2012	772	18000*	>2.56	>10600	−130	− 900	<−11500
Station 20	.....	5635	.....	0	8390*	.1254	475	18000*	2.65	11810	−210	− 680	−12500
Woods Hole	.....	5360	.....	0	.....	.....	235	17840	.084	0	− 60	.....	− 295
Station 1	.....	5670	.....	0	.....	.....	1227	17800*	.410	0	−110	.....	−1337
Station 3	.....	5640	.....	0	13460	.519	1607	17800*	>.720	>1843	−170	−1780	<−3620
Station 2	.....	5440	.....	0	11000	.550	1722	17800*	>.849	>1725	−200	−1920	<−3650
Mathews	.....	5099	.....	0	7294	.309	1102	19725	.672	1001	+ 15	−1087	−2088

* Values taken either by assumption or by interpolation from Figure 31.

Table 4 shows the stations of the Woods Hole section, together with the position and depth of water for each. The method of procedure used here was identical with that described for the preceding section.

TABLE 4.—*Refraction stations, Woods Hole section*

Station	North Latitude	Statute miles south of 42nd Parallel	Depth of water (ft.)
Woods Hole	41°31.2′	33.2	60
Station 1	41°09.8′	57.8	110
Station 3	40°57.2′	72.3	170
Station 2	40°43.4′	88.2	200

STATIONS

Woods Hole.—Figure 33 shows the travel-time curves for all stations of the Woods Hole section. The first measurement was made while the ship, *Atlantis,* on which the recording instruments were installed, was at dock in Woods Hole. It is a good measurement, which yields a normal velocity of 17,840 ft/sec for the crystalline rocks. The water wave was notably weak on all shots at this station, probably because the water in the harbor was shallow, and the bottom was irregular.

No. 1.—The measurement for No. 1 station is incomplete. The U branch of the travel-time curve is well determined, but there is available only a single point for determining the remaining branches of the curve. The data do not suffice to determine whether the first arrival on the longest shot is an S or a C phase, so calculations are made on both assumptions. By assuming it to be an S phase, and taking the velocity in S to be 11,000 ft/sec, according to interpolation from Figure 31, the thickness of the unconsolidated zone is found to be 960 feet. On this assumption, a crystalline zone, with velocity 17,800 ft/sec, would have to be at least 1830 feet below sea level in order to escape detection by the longest shot of the station.

On the other hand, if the first arrival on the longest shot is assumed to be a C phase, whose velocity is considered to be 17800 ft/sec, by interpolation in Figure 31, the depth to the crystalline rocks is 1230 feet. This last result is accepted as the proper interpretation of the data, because it appears to be more concordant with the facts and probabilities, as shown in Figure 32.

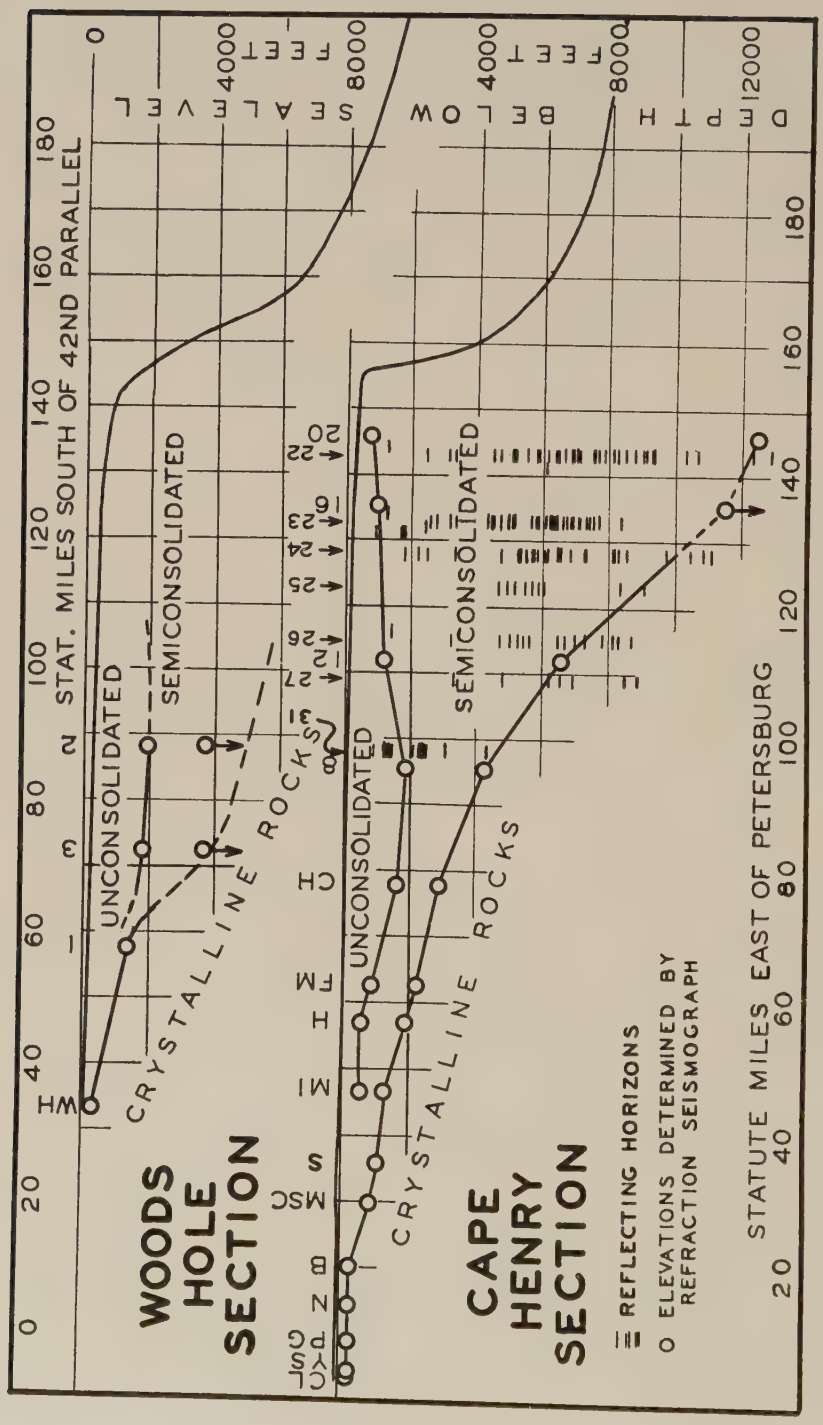


FIGURE 32.—*Cape Henry and Woods Hole sections*

No. 3.—The measurement at No. 3 station is incomplete. None of the velocities is well determined. The observed velocity of 13,400 ft/sec is considered to be the S phase and too large, because of experimental error. On this interpretation, it is necessary that the crystalline zone be at least 3600 feet below sea level in order to escape detection by the longest shot of the station.

No. 2.—The U phase is well determined at No. 2 station. The observed velocity 11,000 ft/sec is considered to represent the S phase, despite the fact that this velocity is much higher than that found for S on the Cape Henry section. Presumably, the crystalline rocks, whose velocity is assumed to be 17,800 ft/sec, are too deep to be detected by the longest of the shots. In that case, they must be at least 3600 feet below sea level.

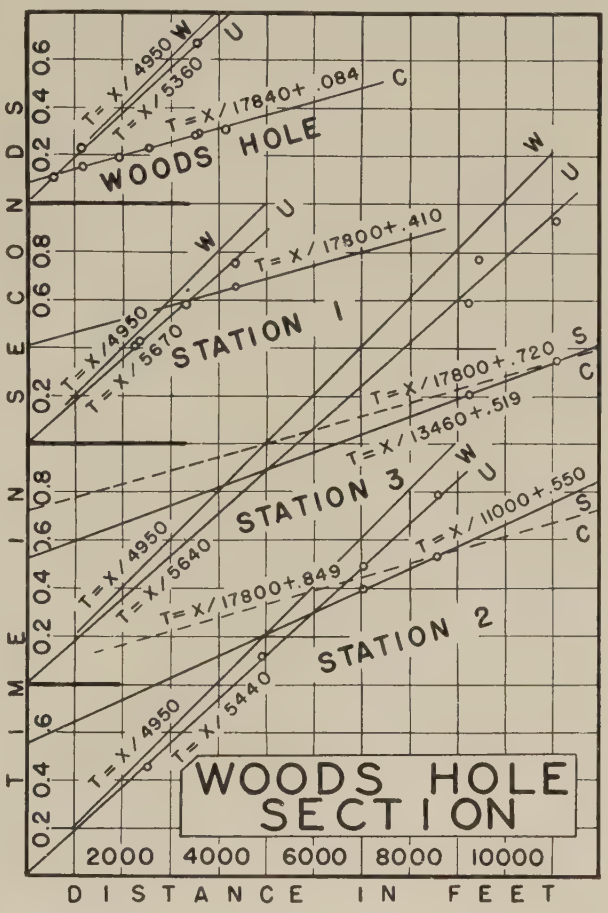


FIGURE 33.—*Travel-time curves for Woods Hole section*

SUMMARY

Tables 2 and 3 contain the travel-time data, the calculations, and the results for the Woods Hole section. The results are shown graphically in Figure 32. Although these results are incomplete, it is possible to make a useful comparison with those from Cape Henry in regard to the thickness of the unconsolidated zone. The two sections, as arranged in Figure 32 for ready comparison of points at equal distances from the outer edge

of the shelf, show that all results obtained at Woods Hole are in good agreement with those from Cape Henry.

The velocity 17,800 ft/sec for crystalline rocks, which was obtained at Woods Hole, is in fairly good agreement with values found by Ewing in earlier work on the granites of this general region: [9]

	Velocity of longitudinal waves ft/sec
Quincy (Mass.) granite	16260
Westerly (R. I.) granite	16400
Rockport (Mass.) granite	17800

REFRACTION MEASUREMENTS AT MATHEWS, VIRGINIA

One long refraction profile and several shorter auxiliary profiles were made in the vicinity of Mathews, Virginia, where a deep bore-hole had reached the crystalline rocks at a depth of 2307 feet beneath the surface, or 2297 feet below sea level.[10] The location of the bore-hole and the positions of the seismic stations are shown in Figure 34.

This locality differs from the others discussed in the present work in having a thin bed of moderately high velocity material (8000 to 10,000 ft/sec) at a depth of 70 to 100 feet. This bed causes the first arrival on the three points between 1000 and 2000 feet on the main travel-time curve and is clearly displayed on the auxiliary curves for locations H and I, as shown in Figure 35.

The wave that travelled through this bed is entered in Table 2 under the heading SH. It was easily recognizable on the seismograms, by its small amplitude, its sinusoidal character and gradual beginning, and its habit of gradually disappearing for long distances. Its behavior with increasing distance led to the conclusion that the bed through which it travelled was thin. The depths calculated for this bed at the various stations are:

Station	V_1 (ft/sec)	V_2 (ft/sec)	T (sec)	h (ft)
Mathews	5099	10000	0.034	101
Location I	4386	9091	0.027	68
Location H	4300	7950	0.028	72

The log of the well reports iron-cemented gravel at 83 to 200 feet depths. It is reasonable to associate the bed detected by the seismic measurements with this horizon. This bed is considered to be so thin that it may be neglected altogether in calculation of depths to underlying horizons.

[9] L. D. Leet and M. Ewing: *Velocity of elastic waves in granite*, Physics, vol. 2 (1932) p. 160.

[10] W. C. Mansfield: *An oil-prospecting well near Havelock, North Carolina*, N. C. Dept. Conserv. Devel., Econ. Pap. no. 58 (1927) 19 pages.

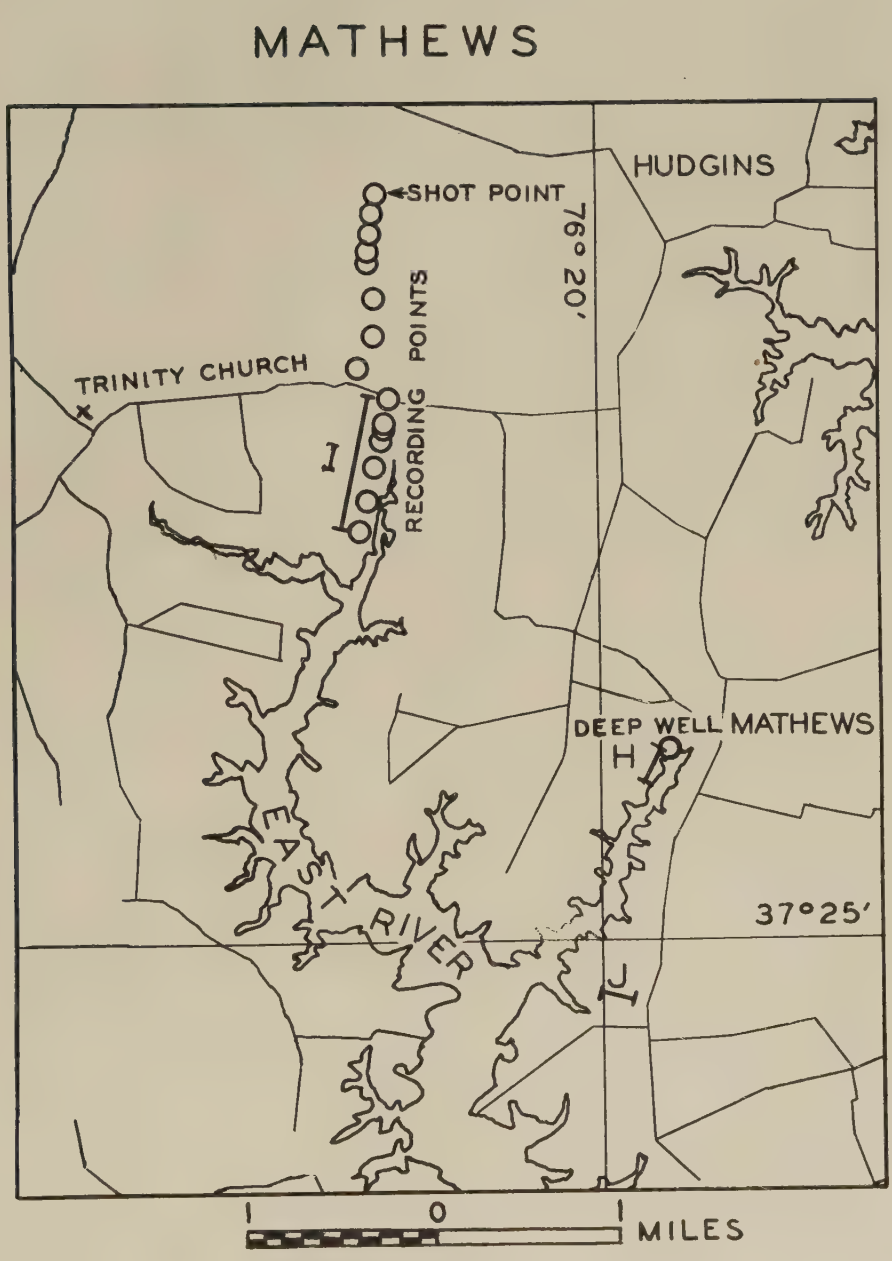


FIGURE 34.—*Station map for Mathews*

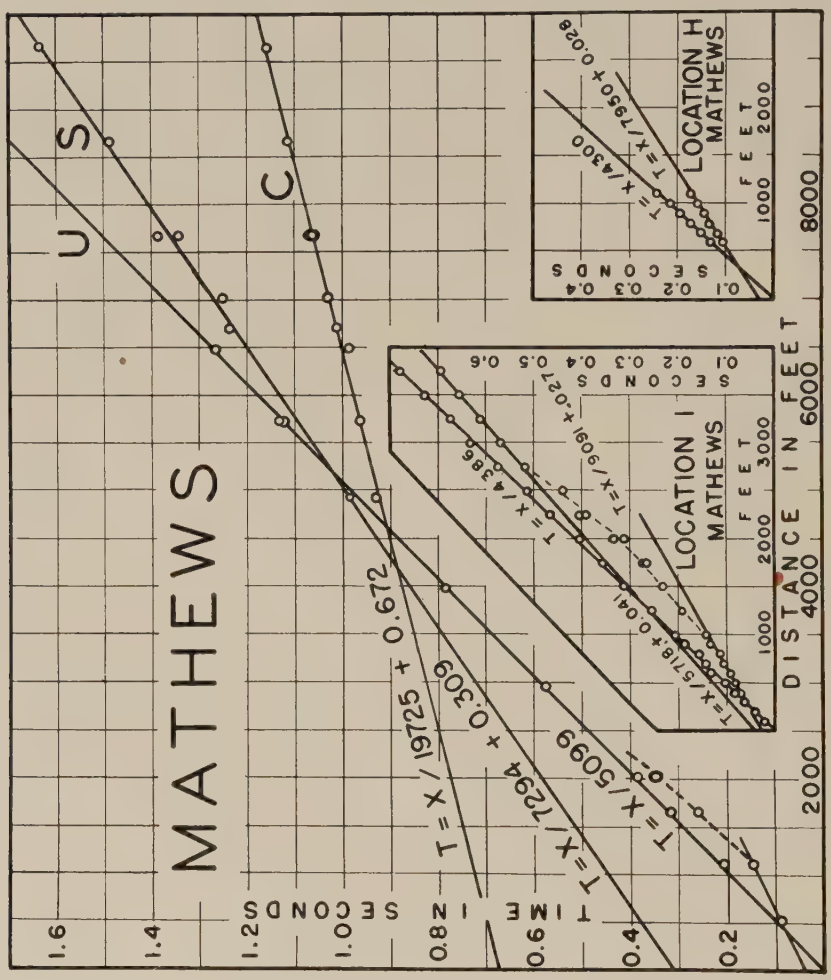


FIGURE 35.—*Travel-time curves for Mathews*

On the Mathews profile, the phases U, C, and S are present, as they were on the stations of the Cape Henry section. The seismograms are of good quality, and all phases that have been plotted may be definitely identified. The travel-time data and the depth calculations are shown in Tables 2 and 3. If this station were projected to the Cape Henry section, it would lie in the vicinity of the Hampton and the Fort Monroe stations, and the elevations found for the semi-consolidated and the crystalline zones would be in agreement. To compare the elevation —2088 feet, found for the crystallines at the Mathews Station, with the —2297 feet, found in the bore-hole at Mathews, it is necessary to make allowance for the fact that the station is about 2½ miles from the well. Assuming the regional slope in the surface of the crystalline rocks to be

the same as that found in the vicinity of Fort Monroe (Fig. 32), the change in elevation between the two points is estimated at 140 feet. This reduces the discrepancy in the seismic result to about 70 feet. The discrepancy would have been large, had the S phase, which is masked, been overlooked.

SEISMIC REFLECTION MEASUREMENTS ON LAND

At Hampton, and also at Mathews, attempts were made to obtain reflections from the surface of the crystalline rocks. Although a few poor reflections were recorded from points within the semi-consolidated material at Hampton, these tests were almost completely unsuccessful. It was not practical, with the facilities available, to bury the explosive deeper than 15 or 20 feet, so the failure may have been caused by surface disturbance and "ground roll", which would have been eliminated by deeper shot holes, similar to those commonly used in land work. It also seems probable that the crystalline rocks in this region do not present an efficient reflecting surface for seismic waves.

SEISMIC REFLECTION MEASUREMENTS AT SEA

METHOD OF OPERATION

Seismic reflection tests at sea were made at the stations marked 22 to 39 in Figure 2. The *Oceanographer* was used for stations 26A, 27A, 28-39, and the Atlantis for stations 22-27. The apparatus used was the same as that described in connection with the refraction measurements.

In all reflection tests made at sea, three geophones were used, one at the bow of the ship, one at the stern, and one midship. The geophones were connected through transformer-coupled amplifiers to the three galvanometers in one oscillograph, which was used to produce a high-magnification record. The other oscillograph was used to produce a low-magnification record by shunting all its galvanometers and connecting each of them in series with the corresponding galvanometer of the first oscillograph. The use of two degrees of magnification doubled the range over which the amplitude of recorded motion was suitable for showing the presence of reflected waves.

In making a test, the three geophones were simultaneously lowered to the bottom from their positions along the length of the ship. The bomb was placed on bottom, at a distance of 100 to 1000 feet astern. As soon as the geophones were on bottom the bomb was exploded electrically by means of a circuit controlled by the operator of the recording apparatus. The firing current was adjusted to require about one-tenth second for producing detonation, and the instant at which the circuit through the deto-

nator was broken was recorded on the seismogram and taken as the instant of the explosion. Bombs for holding T. N. T. were made from 6 by 1½-inch iron pipe nipples, closed at one end by a cap and at the other by a reducer and packing gland, through which the leads to the

TABLE 5.—*Reflection stations at sea*

Station	Statute miles east of Peters-burg	Depth of water (ft.)	Time in un-consolidated zone (sec.)*
26A	131	108	0.30
27A	130	120	0.30
28	131	126	0.30
29	151	282	0.12
30	142	204	0.21
31	98	66	0.59
32	116	90	0.37
33	132	144	0.29
34	142	186	0.21
35	147	246	0.15
36	134	138	0.28
37	153	312	0.10
38	149	246	0.14
39	72	36	0.50
22	143	162	0.20
23	133	120	0.29
24	128	90	0.31
25	123	84	0.34
26	115	84	0.37
27	109	72	0.43

* These values computed from the refraction results shown in Figure 32.

detonator were introduced. In the later experiments, a waterproof gelatin explosive was used, which eliminated the necessity for waterproof bombs. In the first tests the bomb was thrown overboard while the ship was being brought to a stop, the three geophones were dropped as soon as the ship was completely stopped, and the test was made within two or three minutes thereafter.

Captain N. H. Heck devised a method of making reflection tests while the ship was anchored. The bomb was attached to a float and lowered from the stern of the ship.[11] When the tide had carried the float to the desired distance astern, a trip released the bomb and permitted it to drop

to the bottom. The geophones were then lowered, and the test carried out as already described. This method was of great value, because it permitted repetitions at each station until the proper charge of explosive and the proper degree of amplification for best results had been determined.

In the reflection work done on the *Atlantis,* the bombs were carried astern, while the ship was at anchor, by a crew of men in a whaleboat. The whaleboat remained at its station until all necessary repetitions had been made. This method was by far the most satisfactory of those tried, but it would have been impractical to use it in rough weather.

METHOD OF INTERPRETATION

A wave returning to the surface as an echo from a horizontal reflecting surface at considerable depth is identified on a seismogram by the fact that its travel-time is practically the same as that for geophones set at varying distances from the shot point. The total spread of the geophones was 110 feet on the *Atlantis* and almost 200 feet on the *Oceanographer,* and the shot was placed at distances of 100 to 1000 feet from the nearest geophone. Within the limit of accuracy of the present work, it is permissible to consider, in making calculations of depth, that the reflected waves travel vertical paths.

The velocities in the two uppermost zones and the thickness of the upper one are considered to have the values given for them by the refraction measurements, as recorded in Figures 31 and 32. The elevation of a reflecting surface in the semi-consolidated zone is calculated from the equation,

$$E = h_w + h_u + \tfrac{1}{2}\left(T - \frac{2h_u}{V_u}\right)V_s$$

where

E = depth (below sea level) of reflecting surface
h_w = depth of water
h_u = thickness of unconsolidated zone
T = travel-time of reflected wave
V_u = velocity in unconsolidated
V_s = velocity in semiconsolidated
$2h_u/V_u$ = time in unconsolidated.

RESULTS

The stations at which reflection measurements were made are shown in Figure 2 and are listed, with accompanying data, in Table 5. Each station is projected to the line of the Cape Henry section, and the dis-

[11] N. H. Heck: *Sounding to granite,* U. S. Coast Geodet. Surv., Field Eng. Bull., vol. 9 (1935) p. 62.

TABLE 6.—*Reflection tests at sea*

Shot No.	Station No.	Distance (ft.)	Charge (lb.)	Amplifier (stages)
50	26A	.....	0.5	3
51	"	.....	"	2
52	27A	.....	"	"
53	28	.....	"	"
54	"	.....	"	"
55	29	.....	"	"
56	30	.....	"	"
57	31	.....	"	"
58	"	.....	"	"
59	"	.....	det	3
60	"	.....	"	"
61	"	.....	0.5	"
62	32	.....	"	2
63	33	.....	"	"
64	34	.....	"	"
65	35	.....	0.2	"
66	36	.....	0.5	3
67	"	.....	det	"
68	"	.....	"	"
69	"	.....	0.3	2
70	37	.....	0.5	"
71	38	.....	"	"
72	39	.....	det	3
36	22	500	0.5	"
37	"	550	0.3	"
38	"	600	0.3	"
39	"	500	0.5	"
40	"	"	"	"
41	"	1050	2.0	"
42	"	"	"	"
43	23	850	"	"
44	"	900	"	"
45	24	800	"	"
46	"	750	10.0	"
47	25	700	2.0	"
48	26	600	"	"
49	27	700	"	"

tance of the projected point from Petersburg is taken as the coördinate for the station.

Table 6 shows the data on charge of explosive and degree of amplification for each test that was made. The explosive used was T. N. T., 60 per cent dynamite, or, in some cases, only a detonator.

TABLE 7.—*Depths measured by reflections*

Reflection time (sec.)	Elevation reflector (ft.)
(Shot 53)	
0.28	920
0.38	1690
(Shot 54)	
0.39	1730
(Shot 57)	
0.41	1220
0.48	1420
0.68	2050
0.80	2500
(Shot 58)	
0.29	860
0.42	1250
0.48	1420
(Shot 59)	
0.42	1250
(Shot 60)	
0.41	1220
0.45	1340
(Shot 61)	
0.48	1420
0.79	2460
0.96	3100
1.30	4360
(Shot 62)	
0.44	1400
(Shot 63)	
0.66	2400
(Shot 64)	
1.58	6120
(Shot 66)	
1.11	1250
(Shot 38)	
1.47	6010
(Shot 39)	
0.61	2430
1.43	5850
1.51	6180
1.57	6430
1.63	6680
1.74	7140
1.84	7560
2.14	8800
2.23	9170
(Shot 40)	
1.10	2460
1.16	4720
1.26	5130
1.57	6430
1.70	6970
1.85	7600
1.92	7890
2.27	9390
(Shot 41)	
1.26	5130
1.44	5890
1.58	6470
1.72	7050
1.87	7680
2.01	8270
(Shot 42)	
0.78	3140
0.84	3390
0.90	3640
1.26	5130
1.36	5560
1.70	6970
1.98	8140
2.07	8520
2.20	9050
2.28	9390
2.49	10270
2.59	10670
2.99	12340
3.10	12920
(Shot 43)	
0.70	2580
0.74	2750
0.89	3360
1.17	4500
1.28	4940
1.34	5180
1.49	5800
1.55	6030
1.63	6360
1.75	6840
1.82	7140
(Shot 44)	
0.84	3160
0.93	3520
0.96	3640
1.03	3920
1.12	4300
1.16	4460
1.22	4700
1.28	4940
1.34	5180
1.50	5840
1.60	6240
1.65	6440
1.89	7420
1.93	7580
1.97	7750
2.13	8400
(Shot 45)	
0.52	1770
0.62	2200
0.69	2480
0.90	3320
1.40	5340
1.51	5770
1.59	6090
1.71	6570
1.88	7260
2.14	8300
2.21	8530
2.51	9790
2.68	10460
(Shot 46)	
1.26	4760
1.39	5290
1.44	5490
1.53	5850
1.69	6490
1.80	6850
1.89	7300
2.09	8100
2.78	10860
2.85	11160
(Shot 47)	
1.07	3910
1.26	4660
1.33	4940
1.39	5180
1.47	5490
1.52	5690
1.60	6010
2.20	8380
2.38	9100
(Shot 48)	
0.92	3270
0.97	3470
1.30	4750
1.37	5020
1.44	5290
1.48	5440
1.53	5640
1.75	6500
1.81	6730
1.88	7000
1.96	7310
2.10	7860
2.18	8180
2.23	8370
2.33	8760
(Shot 49)	
0.97	3340
1.04	3620
1.09	3800
1.35	4800
1.72	6210
1.81	6560
1.91	6930
2.32	8500
2.41	8850

Table 7 shows the travel-times of the reflected waves that were recorded in each test and the depths of the reflecting surfaces which were calculated from them. The position of these surfaces is indicated by short horizontal marks in Figure 32.

CONCLUSIONS

A striking feature of the reflection results is the great number of reflecting surfaces revealed. Some of the identifications of phases on the seismograms as reflections may be open to question, but many of them are uncommonly good. It is concluded that there are numerous

horizons in the semi-consolidated zone at which slight variations in composition or lithification of the sediments are sufficiently abrupt to produce measurable reflections of the elastic waves. If several tests were made at a single station, it is the general rule that the reflections that look best on one record are also prominent on the others, but there are disappointing exceptions to the rule. The object of the repetitions was to find a combination of operating conditions that would cause one reflection—that from the surface of the crystalline rocks—to stand out with such prominence that it could be identified unmistakably, and, consequently, variations were introduced intentionally into the conditions of each test at a given station (*see* Table 6). As no reflection was found that could be identified with the surface of the crystalline, it will probably not be possible to map the crystalline in this region by reflections.

Some tentative correlations of the more prominent reflections from one station to the next have been attempted, but the stations are so far apart that no result reliable enough for publication has been reached.

To account for the ease with which reflections were observed at sea, in contrast to the difficulty experienced in detecting them on land, it is suggested that the water and the sediments of the unconsolidated zone are sufficiently similar in elastic properties to behave as a single medium. Then, at sea stations, the bomb and, also, the geophones are far enough away from the free surface of the medium to escape disturbance from surface effects. The data on velocities and the absence of "ground roll" in refraction measurements at sea support this view.

The reflections obtained from points within the semi-consolidated zone are good enough so that structure within the semi-consolidated zone could be studied and mapped in this region by the reflection method.

From Figure 32, it is seen that the reflection results give good qualitative support for the section constructed from refraction measurements. At stations 22-25 and 31, reflections are obtained to depths approximately equal to those given for the crystalline rocks. At stations 26 and 27 the reflections have been picked from points considerably beneath the indicated position of the crystalline surface. The deeper reflections for these stations are somewhat questionable in appearance. In general, the part of the section from which reflections are reported coincides reasonably well with the part which had been classified as semi-consolidated from the refraction results.

SUMMARY

The refraction seismograph and the reflection seismograph were successfully adapted for work at sea in depths up to 100 fathoms.

Refraction measurements on land and at sea near Cape Henry, Vir-

ginia, and Woods Hole, Massachusetts, determined the configuration of the surface of the basement crystalline rocks, from the foot of the Piedmont Plateau to the edge of the Continental Shelf (Fig. 32). The thickness of unconsolidated and semi-consolidated material (velocity of longitudinal waves about 8000 ft/sec) near the edge of the Continental Shelf was found to be about 12,000 feet.

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Contribution No. 111

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THE EEL-GRASS SITUATION ALONG THE MIDDLE ATLANTIC COAST *

Each spring since the extensive, epidemic wasting of the common marine eel-grass, *Zostera marina* L., five years ago, there have been anxiously optimistic reports of its reappearance at numerous points. Correlating these indicates a steady increase in the number of new beds and the extension of refoliated range, but no estimate may be had from them concerning the ecological value of this progress. It is certain that the plant persists abundantly through the summer in only a few localities; usually the leaves, badly spotted and marked by lesions associated with the parasitic *Labyrinthula,* slough away in early summer to leave sparsely developed stems and a few seed producing plants of little significance as winter food for migratory waterfowl, in protecting dependent small

* Contribution 111, Woods Hole Oceanographic Institution.

animal forms, or in holding the bottom against erosion.[1] Some notable exceptions, the estuaries of Chesapeake Bay, Shinnecock Bay, L. I., and Great Bay, N. H., have been remarked, where thick grass has abounded through the epidemic.[2] Strangely, the grass in these regions has been heavily parasitized, but seems to grow with such vigor that the wasting has been offset.

The impression gained from investigations of the *Labyrinthula,* the protozoan parasite producing the wasting, is that the presence of plants in the spring is no indication of the bed's continuance through the summer. During the warm months the organism is extremely active and may destroy plants within a few days after spotting or streaking symptoms develop. In anticipating the eel-grass' fate, it would be desirable to know the extent of new beds, the proportion of seedling plants, whether or not the specific parasite is present and active, and seasonal conditions that may be related to vegetative growth.

Early in June, hoping to discover something of these factors, a short intensive, field search was made of the shallow bays from Greenwich, R. I., to Great Bay, N. J. This was made possible through the kind cooperation of Mr. John L. Lynch of the U. S. Biological Survey.

Along the Rhode Island coast conditions for growth seemed much more favorable than farther south. In Narragansett Bay, proper, at Greenwich and Wickford, however, reports and hurried inspection yielded no eel-grass, a matter of concern since the beds had heretofore furnished excellent natural protection to young lobsters introduced from the state hatcheries. At Point Judith, in Fish Pond and westward in Charlestown Pond, Quanochontaug Pond and Winnapaug Pond, there were scattered plants and small, separated beds from a foot to a yard in diameter. These were in good condition, leaves from ten to fifteen inches long, with only a small proportion showing any symptoms of the disease. Many of these plants, surprisingly, were in seed—an unorthodox condition that applied all along the coast, since it is generally held that *Zostera marina* fruits in mid to late summer following inhibition of vegetative growth by the warming water. Abundant growth of vigorous plants in relatively dense, though scattered beds prevailed in the extensive shallows of the western half of Little Narragansett Bay. The leaves were large—a meter long and a quarter of an inch wide; many plants were in seed. This area presented the most favorable redevelopment observed, though streaking and blackening of the leaves was common.

Along the eastern Connecticut coast the drift and reports indicated scattered beds. In Quimbog Cove and at other points east of Mystic, broad leaves a yard long and numbers of plants in seed, free of symptoms, were found in the drift. But in the deeper, rocky bays near New London, no grass or signs of grass could be found. A number of negative observations were made between Stamford and New Haven.

The situation in the shallow bays on the south coast of Long Island was very puzzling; in these the grass had formerly flourished in great profusion, and since the bottoms are still relatively undisturbed, conditions here would seem exceptionally favorable for seedling plants. Along the western and southern shores of Mecox Bay there were many plants in diffuse beds bearing leaves from eight to eighteen inches long and not so broad as those in Watch Hill Bay, most streaked with brown or black, and many in seed. In a small deep arm at the southeast of the bay a number of very large plants were seen with leaves up to four feet long and three-eighths of an inch broad; these bore the marks of disease.

Dense beds of eel-grass extended from the sandy shoals a hundred yards from shore to the edge of the channel, about half a mile off, along the south of Shinnecock Bay. The leaves were small, from eight to ten inches long and a quarter of an inch wide.

[1] **Renn, C.** 1936. The wasting disease of *Zostera marina,* I. A pathological investigation of the diseased plant. *Biol. Bull.* **70**: 148–158.

[2] **Cottam, C.** 1935. The present situation regarding eel-grass (*Zostera marina*). *U. S. Dept. Agri., Bur. Biol. Surv. Wildlife Res. Manag. Leaflet BS. 3.*

These were much eroded and marked by the disease, yet they formed relatively large beds, five feet in diameter, underlaid by firm mats of stems in good condition. From a tenth to a quarter of the plants in these beds were in seed. The growth prevailed in the southern shallows west to the head of the bay, and was characteristic of the gravelly bottom in western Tianna Bay, joining Shinnecock on the north.

These beds, despite the prevailing symptoms of disease, had apparently persisted through the epidemic. Specimens have been received each year from this area, and the current plants may be traced back to stem stock two seasons old. Similarly, the more scattered plants in Mecox Bay were derived from old stem stock; very few of any plants were seedlings.

The southern shallows of Moriches Bay, and of Quantuck and Ogden Ponds, which connect Moriches with Shinnecock Bay through the Interstate Canal, were entirely free from growing grass. On the wide flats to the north and west of Fire Islands in Great South Bay there were uniformly scattered plants and some very small clumps, but no beds to speak of. These plants, too, were from old stock. They were small and almost altogether free from symptoms of disease—possibly related to their retarded growth through a layer of fresh silt two to three inches deep that covers this area. A few of these plants were in seed. The shallow to the north of the channel from Fire Islands to Jones Beach appeared free of eel-grass, though occasional floating leaves were noted.

In Barnegat Bay, intensively explored along the south shore, there were scarcely any plants, and no small areas comparable to any of the foliated regions of Long Island. Small, spotted leaves and seed plants were found in the drift near Tom's River, but no living plants could be discovered to the north of Barnegat Inlet. About half a mile south of the Inlet, below Barnegat City, there were a few scattered plants, not more than a hundred in all. And on the shallows near Lovelady several small beds were discovered, all plants free from any trace of disease, and bearing narrow leaves about eight inches long. Several seed plants were found among them. Fishermen and clam diggers along the south shore reported the almost complete absence of the grass; shallow trawls came up with few leaves. On the other hand, there appeared to be, even early in the season, a considerable drift of leaves through Barnegat Inlet on the ebb tide, to judge by fouled anchor ropes and fishing lines. But it is certain that very few growing plants have been seen anywhere in the Bay. This is also true of the western shore where a number of searches and enquiries were made, the only successful haul being seven leaves that turned up in an order of steamed-clams, reputedly from Tuckerton Harbor.

Specimens of diseased plants were taken from all beds and examined microscopically for the parasitic *Labyrinthula,* and also for the *Ophiobolus* reported by Mounce, Tutin, and Petersen as present in Canadian, British, and Danish grass.[3] The *Labyrinthula* was present without exception in grass showing spotting or streaking. Two specimens from Shinnecock Bay bore a very sparse development of fungus mycelium, but none showed pycnidia characteristic of fungus infection described by the above investigators. The parasite, then, is present everywhere in the area studied, and presumably will become more active through the summer.

A second feature of significance is the scarcity of seedlings in the foliated areas, indicating the ineffectiveness of spreading by seed as compared with growth from persistent stem stock. From this it may be anticipated that long cool springs, favoring the vegetative phase of the plant's development and permitting the storage of food materials in the stem, will greatly accelerate the spread of the beds. Rapid warming of the water, on the other hand, will be unfavorable in shortening vegetative development and stimulating the parasitic activity of the *Labyrinthula.*

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[3] **Mounce, I., and W. Diehl.** 1934. A new *Ophiobolus* on eel-grass. *Can. Jour. of Res.* **11**: 242.

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SEASONAL PRODUCTION OF ZOÖPLANKTON OFF WOODS HOLE WITH SPECIAL REFERENCE TO CALANUS FINMARCHICUS[1]

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The purpose of the work described in this paper was the investigation of the distribution of the plankton in the waters around Woods Hole during the summer months and the study of the seasonal changes in the plankton at one locality throughout an entire year. Our primary object specifically was to ascertain whether the copepod, *Calanus finmarchicus*—a form used extensively for laboratory experiments—breeds in this region, and if so during which months and with what success. It was proposed also to include measurements of the physical and chemical factors in the environment, and the collection of nannoplankton and phytoplankton, in order that the sequence of biological events from season to season in this locality might be followed. Cause and effect relationships in the growth of the various plankton forms might thus be unraveled.

Since copepods play a prominent rôle in the economy of the sea, it is important to know what conditions promote their growth and what factors tend to reduce their numbers (Clarke, 1934). To this end a series of laboratory experiments was initiated in which the nutrition of copepods, particularly of *Calanus finmarchicus*, was investigated (Clarke and Gellis, 1935; Fuller and Clarke, 1936; and Fuller, 1937). The nearest point from which copepods of this species could be obtained in sufficient numbers was in the deeper water off Gay Head. The population of *Calanus* at this locality was found to persist throughout the summer, but we had no knowledge either of the subsequent fate of these copepods or of the time and conditions of their appearance here. In our studies of nutrition we had assumed that the *Calanus* found in this area were living in equilibrium with their environment and that the smaller organisms found in the same body of water were adequate both qualitatively and quantitatively for their food supply. If, however, these copepods had been produced in another locality and transported hither by currents, the possibility existed that the conditions at our point of observation were not suitable

[1] Contribution No. 112, Woods Hole Oceanographic Institution.

for the growth or even the maintenance of *Calanus* and that the copepods found here were destined shortly to die off. The proposed field observations were therefore especially desired and when worked out in conjunction with further laboratory experiments should eventually yield information on the factors controlling copepod production which would have a general application.

Let it be understood, however, that the work described in this paper was of the nature of a reconnaissance program. The locality chosen for the observations throughout the year was a point as far offshore as could be reached within a day's sail from Woods Hole, but it probably is not entirely removed from fluctuating land influences. However, evidence will be given below for believing that this station is typical of a considerable area.

Location of Stations and Hydrography

During the summer of 1935 the five stations in the waterways around Woods Hole shown in Fig. 1 were visited about twice a week. Buzzards Bay is a broad, shallow body of water with a temperature a few degrees higher and a salinity slightly lower than Vineyard Sound. A strong current flows in Vineyard Sound, and offshore water seems to be carried into the Sound much more readily than is the case with Buzzards Bay (Haight, 1936). Since access to the open sea from Woods Hole is most direct through the western entrance of Vineyard Sound, a line of stations was run in that direction to study the transition between inshore and offshore conditions and populations.

Station 3, which was selected for the continuation of the observations throughout the year, was visited once a month during the autumn and winter and at least twice a month from April to September. The authors are indebted to Dr. Renn, Mr. Iselin, Mr. Woodcock, and Mr. Butcher for assistance which made these trips possible. A rough sea is almost always encountered at the exposed location of Station 3, and during the extremely cold weather when spray froze on the deck and rigging, work was extremely difficult.

Station 3 is about eight miles from the nearest points of land on the north and east, and twenty-five miles from Block Island on the west. On the south the continental shelf water extends without obstruction. Since at Station H2 (see Fig. 1) the flood tide flows NNE and the ebb tide flows WSW, the main body of water debouching from Vineyard Sound and Buzzards Bay probably passes largely to the west of Station 3. However, the currents in this region are extremely complex and unfortunately the measurements of the U. S. Coast and Geodetic Survey (Haight, 1936) do not extend as far out

FIG. 1. Location of Stations 1–5 at which plankton hauls were made, and of Station H2 occupied by the U. S. Coast and Geodetic Survey. The small island of No Man's Land lies just off the map to the south of Gay Head. Buzzards Bay comes to an end just north of the limit of the map, whereas Nantucket Sound is open to the sea on both sides of Nantucket Island.

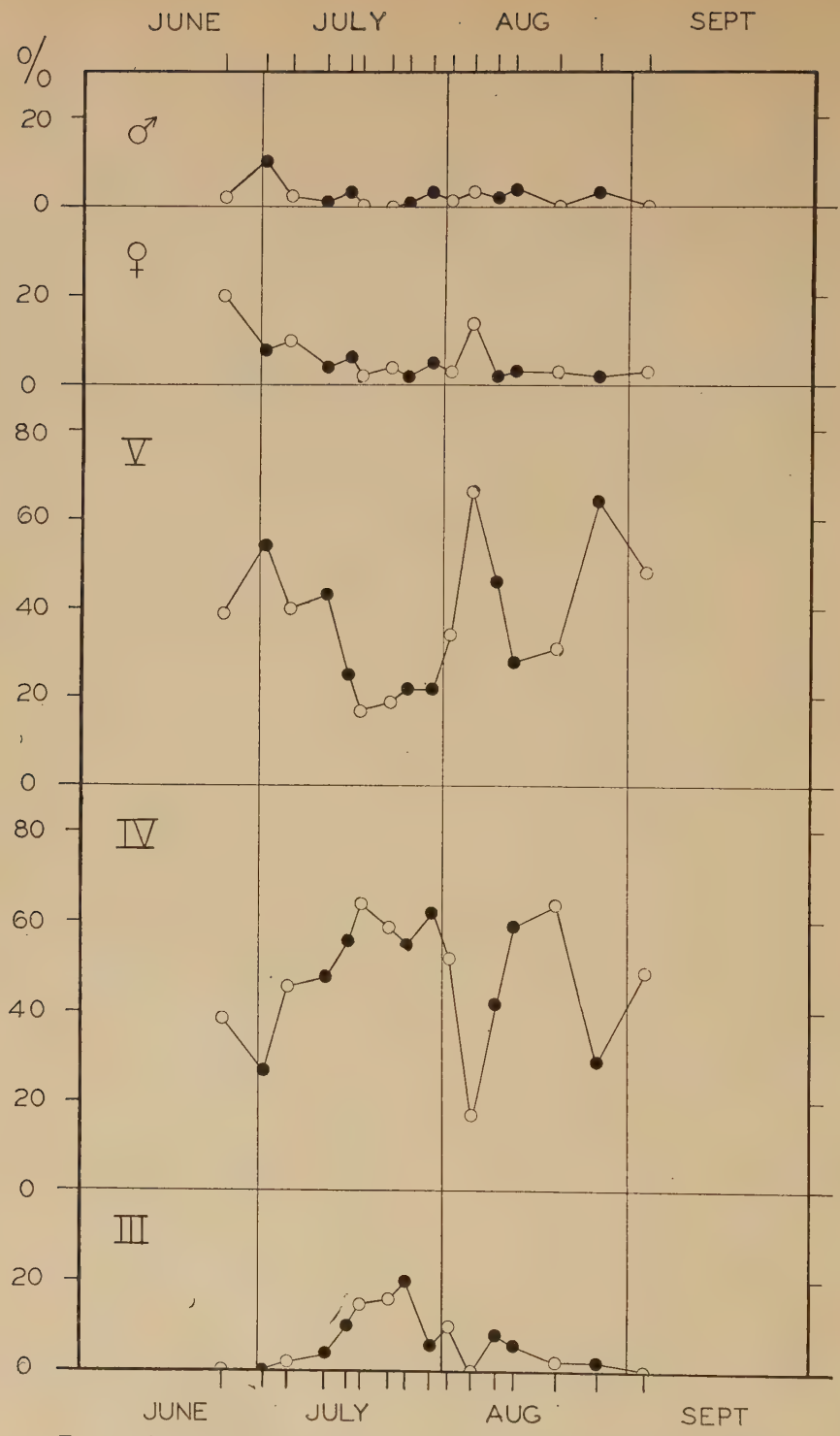

FIG. 2. Percentage distribution of *Calanus finmarchicus* copepodid stages III, IV, and V and adult ♀ and ♂ taken with the scrim net at Station 3 during the summer of 1935. The open circles represent catches made on an incoming tide (E. 1 hour–W. 1 hour) and the solid circles represent catches made on an outgoing tide (W. 1 hour–E. 1 hour).

as our station. Our plankton catches during the summer of 1935 at the stations nearer shore showed a considerable difference depending upon whether they were made on an incoming or an outgoing tide. There is some evidence that the effect of the tide was felt as far out as

FIG. 3. The salinity and temperature at depths of 0, 15, and 30 meters at Station 3 during 1935–6. The vertical markers along the abscissa indicate the dates on which observations were made.

Station 2, but at Station 3 no consistent difference due to the phase of the tide was observed, as may be seen for the *Calanus* population from Fig. 2. Transparency measurements similarly indicated the presence

of typical offshore water at this station (Clarke, 1938). However, for the sake of uniformity, our observations throughout the year were made as far as possible only during the periods when the "east," or flood tide, had flowed for at least one hour, and before the "west" tide had flowed for more than one hour.

These tidal oscillations are superimposed upon the much larger but slower coastal current which flows in a southwesterly direction over the continental shelf all along this coast. Water is moving continuously from Nantucket Shoals on toward New York. It is presumably from the inner edge of this current that the water at our station is derived. Yet there must be a certain admixture of inshore water, since the salinity value at Station 3 (see Fig. 3) was slightly lower at all seasons of the year than that characterizing the water farther offshore[2] and was slightly higher than that found within Buzzards Bay and Vineyard Sound, according to determinations which we carried out during the summer of 1935. The prevailing wind, which is from the southwest, would tend to blow offshore water in toward our station, but gales from this direction or from other points of the compass probably disturb the normal hydrographic situation rather profoundly.

The fluctuations in the salinity at Station 3 from July, 1935 to September, 1936, were for the most part confined between 31.5 and 32.5 ‰ and generally uniform at the depths of 0, 15, and 30 meters (Fig. 3). On several occasions, however, a noticeable freshening of the surface layer was observed, and on December 29, 1935, an unusually great difference in salinity existed between the surface and the bottom. Since a pronounced transparency anomaly occurred on the same day (Clarke, 1938), we may assume that an abnormal interchange of water masses took place on this occasion.

The temperature change at Station 3 during the year was extremely great for a marine environment. The maximum value, observed in August, was over 23° C. higher than the minimum value, in February (*cf.* also Allee, 1919). During the summer months the water was highly stratified, for a difference of 8° or 10° was usually found between the surface and the bottom. This would seem to indicate that no great stirring was produced by wind or tide in these months, but it is conceivable that the temperature difference could be brought about by some persistent differential water movement. In September the surface water began to cool off rapidly and to mix more effectively with the bottom water, thus raising the temperature of the latter. By the first of November the temperature had become

[2] At Station "Martha's Vineyard I." See H. B. Bigelow and M. Sears (1935).

uniform from top to bottom. This condition persisted throughout the autumn and winter indicating strong stirring action during this period. In the spring months warming took place more rapidly in the upper layers than in the deeper with the result that a progressively greater difference in temperature was found between the surface and bottom until by June or July a pronounced stratification was re-established.

Methods

During the summer of 1935 10-minute horizontal hauls for zoöplankton were made using the scrim closing nets described by Clarke (1933). At Stations 1, 4, and 5 hauls were made at depths of 2 meters below the surface and 2 meters above the bottom; at Stations 2 and 3 an additional haul was made at a depth mid-way between the other two. Water samples were taken and temperatures determined at each of these depths. A fraction of each water sample was turned over to Miss Lois Lillick for qualitative and quantitative analysis of the phytoplankton. Other fractions of the water samples were bottled for determination of salinity, and of phosphate and nitrate content. The authors are indebted to Mr. Alfred Woodcock, Mr. Bostwick Ketchum, and Mr. Homer Smith, for these chemical analyses.

For the work at Station 3 from October, 1935 to September, 1936, the zoöplankton was taken in "oblique" hauls in which the net was lowered to 30 meters (just over the bottom), towed for 1 minute, then raised 1 meter and towed for 1 minute, then raised another meter and so on, until the surface was reached. A double-action hand plankton pump was added to our equipment in order that the eggs, nauplii, and younger copepodid stages of the copepods, which were too small to be retained by the scrim net, might be caught whenever spawning took place. The free end of the hose was attached to the cable about 2 meters above the weight and then lowered to the bottom. The outflow from the pump was piped directly to a 1″ Hersey Water Meter and then discharged into the top of a No. 20 silk phytoplankton net hung vertically in a metal barrel. Ten gallons (about 38 liters) were pumped at each meter from the bottom to the surface.

At 30, 15, and 0 meters bottles were filled from the hose for the chemical analyses and for quantitative phytoplankton counts by Miss Lillick. At 20, 10, and 0 meters the pump was stopped and the contents of the silk net drawn off and bottled separately, thus dividing the catch into three parts representing three strata in depth. On each occasion temperatures were taken and light penetration was measured as is described elsewhere (Clarke, 1938). When time

permitted, a second oblique zoöplankton haul and pumping operation were carried out to compare with the first. The net hauls and the pump catches were analyzed by suitable dilution and subsampling (Clarke, 1933). Our thanks are due Mr. David Bonnet for assistance in this task and in the preparation of the tables and diagrams.

General Features of the Zoöplankton

The number of species of zoöplankton represented in our catches by one or more specimens is enormous (*cf.* Fish, 1925)—too numerous for detailed analysis in an investigation devoted primarily to the

Table I

Total number of Calanus finmarchicus in hundreds calculated on a basis of a 30-minute haul.

Date 1935	Station 1	Station 2	Station 3	Station 4	Station 5
June 24	6	106	90	—	—
July 1	12	65	142	5	37
5	8	90	109	—	0
8	x	91	—	x	15
11	x	108	216	0	4
15	11	152	123	—	—
17	14	74	124	x	x
22	6	20	209	—	x
25	14	288	147	x	x
29	9	529	267	5	3
Aug. 1	84	385	232	3	0
5	5	52	171	6	6
9	11	25	72	—	—
12	3	92	94	x	x
19	8	137	50	x	0
26	0	28	113	0	0
Average	13.6	140.1	143.9	3.1	7.2

— indicates station omitted.
x indicates less than 100.

study of the production of a few important forms. Even a cursory glance at the material, however, reveals that a considerable difference exists in the plankton at the stations near shore and at those farther out. At Stations 1, 4, and 5 large numbers of larval forms of both bottom-living and pelagic species were encountered mixed in with a varying number of mature individuals of truly planktonic types. The composition of this inshore population changed almost daily in contrast to the more gradual fluctuations which took place offshore.

At Stations 2 and 3 fewer types were found in the plankton and,

although quantities of immature specimens appeared at certain seasons, these belonged mainly to the same species as the adult individuals. The difference in the population offshore is well illustrated in Table I, in which the total numbers of *Calanus finmarchicus* at each station are set forth. *Calanus* was consistently scarce at Stations 1, 4, and 5 and, although the average number at Station 3 was only slightly greater than that at Station 2, a population of at least moderate dimensions was always to be found at the offshore station.

TABLE II

Total zoöplankton taken in scrim net at Station 3, 1935–36. Thirty-minute oblique hauls with 75 cm net. Approximate volumes after settling one month.

Date	Haul No.	Vol. cc.	Av.	Date	Haul No.	Vol. cc.	Av.
Sept. 3	181	<10		May 25	204	240	
	182	<10	<10		205	160	200
Oct. 1	185	105		June 11	206	270	
	186	70	88		207	215	246
No.v 2 (Sta. 2)	187	215		June 25	208	105	
	188	160	188		209	140	123
Dec. 1	189	140	140	July 10	210	70	
Dec. 29	191	105 S			211	90	80
	192	160 S	134	July 22	212	45	
Jan. 27	193	105 S			213	40	43
	194	185 S	145	July 30	214	240	240
Feb. 23	195	700 S	700	Aug. 6	215	210	210
Mar. 27	197	10	10	Aug. 14	216	70	
Apr. 13	198	40			217	70	70
	199	65	53	Aug. 20	218	210	
Apr. 25	200	115			219	160	185
	201	115	115	Aug. 31	221	70	
May 11	202	65			222	40	55
	203	90	78	Sept. 13	223	<10	
					224	10	10

Note: Hauls mostly copepods except those marked "S" which were mostly sagittæ. The net used catches effectively animals as large as, or larger than, copepodid Stage IV of *Calanus finmarchicus*. Many smaller forms are not retained by the net.

The seasonal variation in the total population may be traced from the approximate volumes of the zoöplankton taken at Station 3 throughout the year (Table II). Plankton was scarce during September and October, but increased in November and December. The mid-winter hauls were characterized by large quantities of sagittæ. After this plankton again became scarce, but during the spring months volumes increased reaching a maximum early in June

The plankton remained abundant through the summer with few exceptions until in September a sudden reduction was encountered.

At all the stations Crustacea—usually copepods—formed the bulk of the catch with the exception of a few occasions on which large numbers of medusæ or, at the offshore stations, of sagittæ were encountered. The most common copepods, in addition to *Calanus finmarchicus*, which will be treated in a separate section, were the following (*cf.* also Fish, 1925):

Centropages typicus	July to Dec.	Numerous in August
Centropages hamatus	May to July, and in Sept. and December	Numerous in June and July
Pseudocalanus minutus	Jan. to Oct.	Numerous Mar. to Aug.
Paracalanus parvus	July to Sept. and in Feb.	Numerous in Aug.
Acartia tonsa	April to Dec.	
Oithona similis	April to Sept. and probably throughout the year	
Labidocera æstiva	Oct. to Dec.	

Many of these copepods appear to breed in this region because immature specimens of most of the list were found on one occasion or another. The copepodid stages of *Centropages* (species not determined) were particularly numerous during the summer months, and the locality is a veritable nursery for *Pseudocalanus* as judged by the large numbers of eggs, naupliï, and copepodites taken in the pump catches, particularly in the spring.

Sagitta elegans was represented by at least a few specimens in almost every haul at Station 3 and the large catches of sagittæ reported on several occasions consisted entirely of this species. *Sagitta enflata* occurred in small numbers in October and November, 1935, and in August, 1936. *Sagitta serratodentata* was taken from September to December, 1935, and in August, 1936, and was abundant on only one occasion. It was noticed that the size of *Sagitta elegans* varied greatly from month to month and that the smallest individuals appeared in January, May, July, and September. Since these months agree almost exactly with the four periods of the year during which Russell (1932–33) believes the main breeding of *Sagitta elegans* to take place at Plymouth, we may conclude that the seasonal production of this species is approximately the same on both sides of the Atlantic.

The Production of Calanus finmarchicus

Comparison of Net and Pump Catches

The numerical analysis of our zoöplankton hauls was limited almost entirely to *Calanus finmarchicus*. The numbers of this species taken in the scrim net ran into the tens of thousands. If we assume 100 per cent

straining efficiency, the scrim net filtered 564,000 liters of water during the standard 30-minute haul. In the standard pump operation, on the other hand, the total volume of water delivered to the phytoplankton net in pumping from 30 meters to the surface amounted to 1134 liters. One copepod in the pump catch would theoretically correspond to about 500 copepods in the net haul provided that the two methods are equally effective in catching all stages of *Calanus*. This was not expected to be the case, but since a few of the older copepodites and adults were usually to be found in the pump catches, these older stages were counted as well as the younger stages in order that the sampling efficiency of the pump and the net might be compared.

The total number of each stage of *Calanus* in the pump catches throughout the year is shown by the solid areas in Fig. 4. All the nauplius stages have been lumped together because the duration of each of these stages is short compared to the intervals between our observations. Very few of the earlier nauplius stages were taken. Certain eggs, which may have been those of *Calanus*, were found, but the number of these was so trifling as not to be worth plotting. The scarcity of eggs and early naupliï suggests that the actual spawning ground may be farther offshore than our station.

The numbers of *Calanus* taken in the net hauls is indicated by the superimposed single line (Fig. 4), but using a different scale. The magnitude of the scale which has been used for the net hauls was determined by finding the ratio between the two sets of data for copepodid Stage IV. This stage was chosen for the comparison of the numbers taken with the pump and with the net because it seems to have been caught effectively by both methods. Since the number of *Calanus* in this stage was high both on July 30 and August 6, the average number taken by the net on these two days was divided by the average number taken with the pump. The resulting quotient was very nearly 100. Accordingly all the totals for the net hauls were divided by 100 before plotting. The scrim zoöplankton net should theoretically remove animals from 500 times as much water as the pump. Since the volume of water passing through the pump was accurately measured, we reach the conclusion that the straining efficiency of the scrim net is 20 per cent.

The two curves for Stage IV which have been brought together at one point in the manner described are seen to correspond very roughly for the rest of the year. For copepodid Stage V and for the adults, however, the curves for the pump catches consistently lie below those for the net hauls. This indicates that the latter method is relatively more effective than the former for these larger individuals either

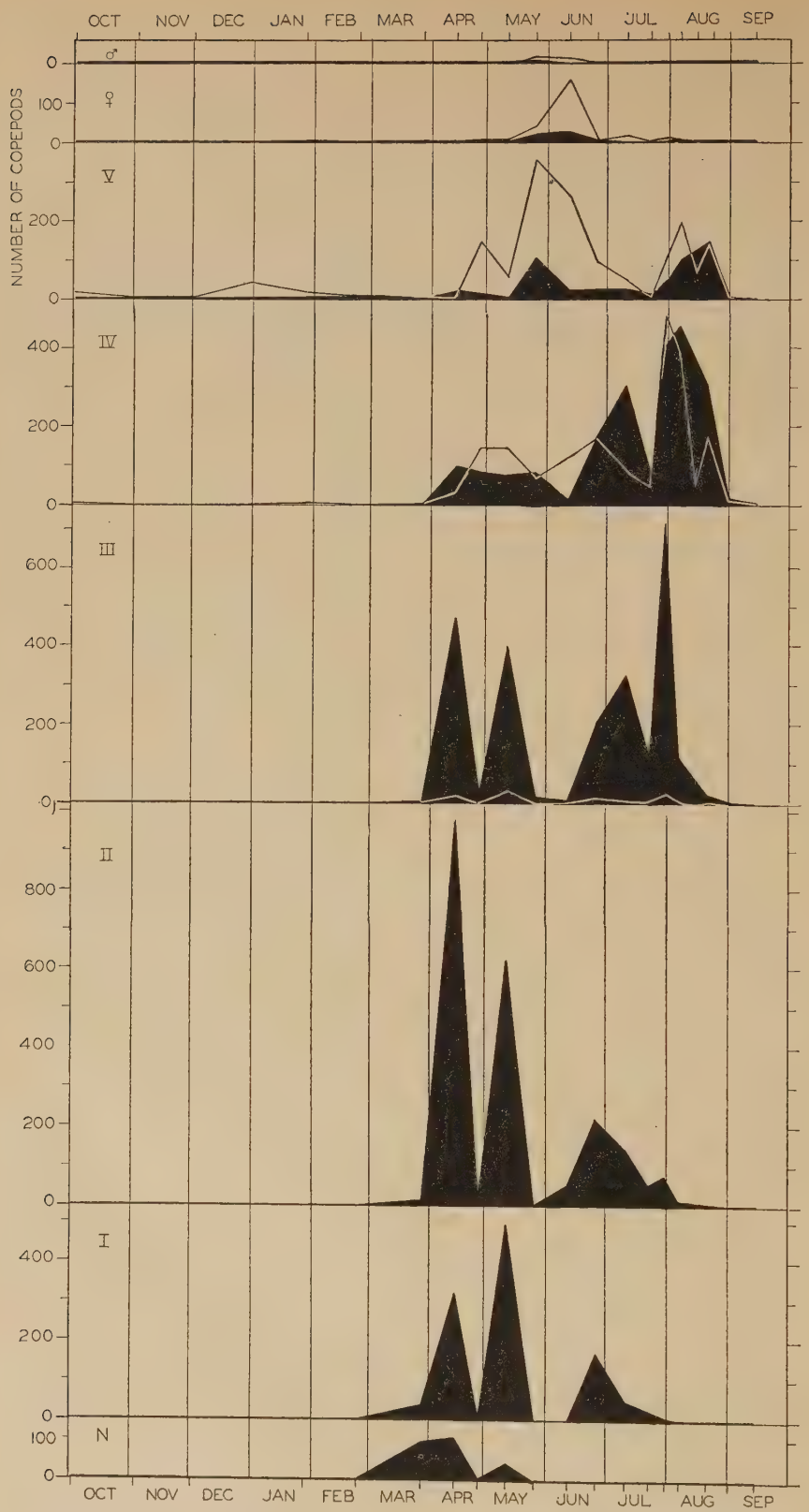

FIG. 4. The solid black area indicates the total numbers of *Calanus* nauplii (N), copepodid stages I–V, and adult ♀ and ♂ taken with the pump per standard haul (see text). The superimposed line shows the numbers of *Calanus* taken with the scrim net per standard haul, but for these the scale must be multiplied by 100.

because fewer slip through the mesh of the net or because more escape the mouth of the hose. The opposite situation is seen in the case of copepodid Stage III in which it appears that a disproportionate number of this group fails to be caught by the net.

Seasonal Changes in Abundance

Nauplii occurred in significant numbers on only three occasions, namely March 27, April 13, and May 11. Copepodid Stages I and II have peaks of abundance on April 13, May 11, and June 25. Stage III was numerous also on April 13 and May 11 and a third period of abundance extended from the end of June to the first part of August. The numbers of individuals in Stage IV were moderate in April and May, increased rapidly in June, and reached a maximum early in August. The net caught representatives of Stage V in every haul throughout the year, but with the exception of December 29, numbers were extremely low from September until the end of April. This stage was particularly abundant at the end of May and again in August, but never equalled the maximum of Stage IV. Adult specimens of *Calanus* were most numerous in May and June, but at all times were relatively scarce, particularly the males. Taking the species as a whole, we may conclude that the population is of very small dimensions during the autumn and winter. By the first of April reproduction has begun and from then on through the summer *Calanus* is abundant. At some time after the end of August the species suddenly becomes depleted and the population is not restored again until the following spring.

Succession of Generations

To determine the number of generations[3] which succeed one another during the year recourse is best made to the percentage distribution of the various age stages within each of the hauls from season to season because this procedure removes the confusing effect of fluctuations in the size of the total catch and allows the progression from stage to stage to stand out in relief. The percentage diagram for the pump catches (Fig. 5) shows that on the first of October the total catch

[3] The term "generation" is used here instead of "brood," which has been employed by others in this connection, because the former word expresses correctly the relationship of the two groups of copepods which appeared during the course of the year. The term "brood" should be limited to its strict sense in order to avoid confusion. Nicholls (1933) regards it possible for each female copepod to produce more than one brood of ova. Accordingly there may be circumstances in which the young of the second generation exist contemporaneously with a late second brood of the first generation. The necessity for using these terms with their exact meanings thus seems obvious.

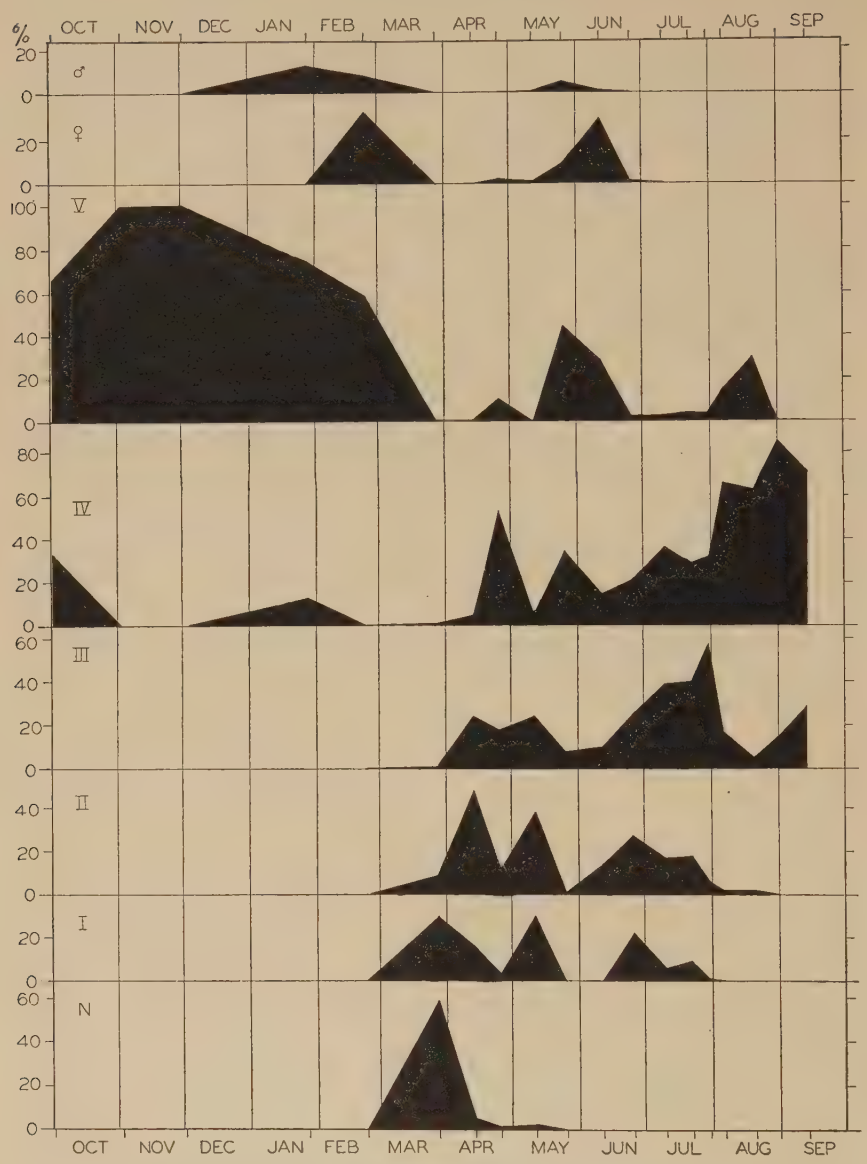

FIG. 5. Percentage distribution of *Calanus* nauplii, copepodid stages I–V and adult ♀ and ♂ taken with the pump at Station 3 during 1935–6.

consisted of 66 per cent Stage V and 34 per cent Stage IV. During November and December practically 100 per cent of the species occurred as Stage V. But in January some of these individuals matured into adult males and in February an even larger proportion of

females appeared. A month later the males and females had largely disappeared and Stage V was reduced to 1 per cent, while nauplii comprised 60 per cent of the catch and copepodid Stage I amounted to 30 per cent. During April other copepodid stages appeared in succession, but these gave rise to only a very small percentage of adult females and practically no males. In May a second series of peaks is to be found progressing up through the copepodid stages and culminating in a peak for the adult males on May 25 and a prominent peak for the females on June 11.

The relationship between these two series of peaks in April and May is obscure. Although we know that in other areas two or more generations may follow one another in rapid succession during the spring and summer, the time interval between our two series appears to be too short for them to represent successive generations. In laboratory experiments Nicholls (1933) found that 27 days was the minimum time possible from the shedding of the ova to the appearance of the adults at the temperature at which he worked (apparently 11–14° C.). The observations of Ruud (1929), Lebour (1916) and Fish (1936) indicate that a longer time than this is required for the entire development of *Calanus*. Marshall, Nicholls, and Orr (1934) state that "the eggs appear after two to four weeks, spawning may last for several weeks, and the adults then die out." Taking fourteen days as the minimum time for the maturation of the eggs and 27 days as the minimum for development, it appears that 41 days is the shortest interval which can exist between the spawning of one generation and the spawning of the next—or between the two generations at any corresponding stage of development. At certain stages in our April and May series the peaks are less than 30 days apart and the temperature of the water at the time was only about 6–8° C. It seems very doubtful, therefore, that the copepodites appearing in May were produced by the individuals which were found as copepodites in April. It is possible that the May group is a late second brood from the same parents as the April group. Adult specimens of *Calanus* were present in the water throughout April although their numbers were low. Another possible explanation of the situation is that at the end of April an unusually extensive movement of water along the coast swept away the population which had reached Stage IV on April 25 and brought in an entirely distinct population of copepods whose development was two or three weeks behind that of the first group. The reduction in the abundance of the first group when it reaches Stage V and its practical disappearance thereafter support this idea (*cf.* Fig. 4).

Another group of Stage I copepodites appeared late in June and

continued into July, but in lesser numbers. In the succeeding weeks the older copepodid stages became numerous one after another until by August 20 a prominent peak had been built up in Stage V. This summer generation was undoubtedly produced by the individuals which we observed as mature adults in May and June, although the

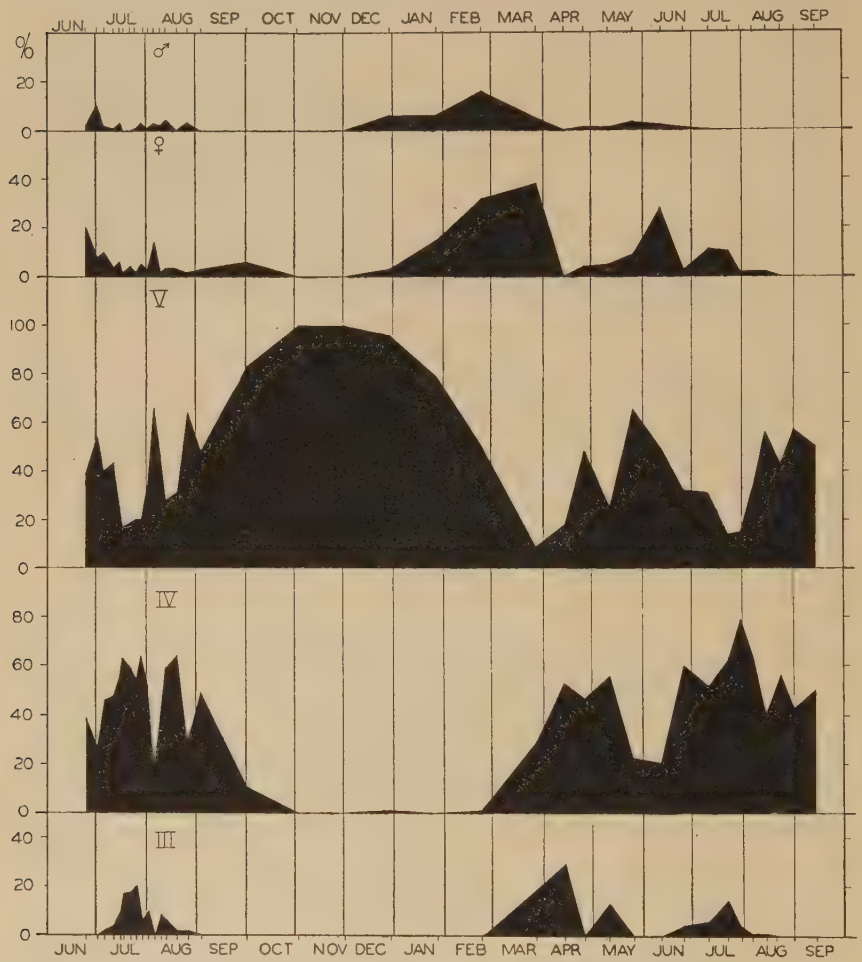

FIG. 6. Percentage distribution of *Calanus* copepodid stages III, IV, and V and adult ♀ and ♂ taken with the scim net at Station 3 during 1935–6.

eggs and nauplii which should have appeared in June were not found. Evidently the spawning took place during the two-week's interval between our visits to the station in June, or else at a point farther offshore. There is some indication in the diagram that this summer

generation consisted of more than one brood, but the irregularities were so great that no definite conclusion can be reached. It seems clear, however, that Stage IV moulted only slowly into Stage V during August and that these individuals did not mature into adults immediately, but formed the population destined to carry over the autumn and winter as Stage V.

The catches with the scrim zoöplankton net have similarly been calculated on a percentage basis to serve as a check on the conclusions reached with the pump catches (Fig. 6). The numbers of the older stages of *Calanus* taken with the pump were low and the possibility existed that the larger individuals escaped the 1-inch opening of the hose, whereas loss from this cause would be much less in the case of the scrim net. Since the net hauls were begun four months earlier than the work with the pump, we have a record for two summers and the intervening winter. At the end of June, 1935, relatively large numbers of adult males and females were found. The spawning of these produced the summer generation which appeared as Stage III copepodites in July. This generation formed the winter stock which did not mature until January, February, or March. Individuals in Stage III appearing in the net hauls in April (with a subsidiary group in May) constituted the spring generation of 1936. This generation matured and spawned in June and we find the summer generation as Stage III in July, thus nicely confirming the net haul results of the previous year.[4] As before, these individuals grew slowly during the summer, and when work was discontinued in September, the population was about equally divided between Stage IV and Stage V.

From both the pump catches [5] and the net hauls we conclude that at Station 3 a short-lived generation of *Calanus* occurs during the spring and is followed by a long-lived generation which has its origin in the early summer and lasts through the following winter. One or more subsidiary groups were found during the spring and summer which may represent second broods from the same adults, or immigrants in a different stage of development, or possibly additional generations of very short duration.

These two main breeding periods correspond closely with those observed by Fish (1936) in the Gulf of Maine for the "western stock"

[4] During the summer of 1937, however, incidental observations showed that the *Calanus* population was extremely small in this region and consisted mostly of Stage V. Evidently annual variations may be considerable.

[5] The fact that the pump catches obtained through a 1-inch hose gave the same general picture of the production of *Calanus* as the net hauls suggests that a device with a relatively small opening is adequate for plankton studies and could be more widely used (*cf.* Hardy, 1936). Such a device would have the important advantage that the volume of water strained could be accurately measured.

of *Calanus*. Fish believes that this stock forms the principal source of supply for the Gulf and he reports that these animals breed chiefly in March–April and in June–July, but possibly also in September. The developmental period of two and one-half months which Fish calcu-

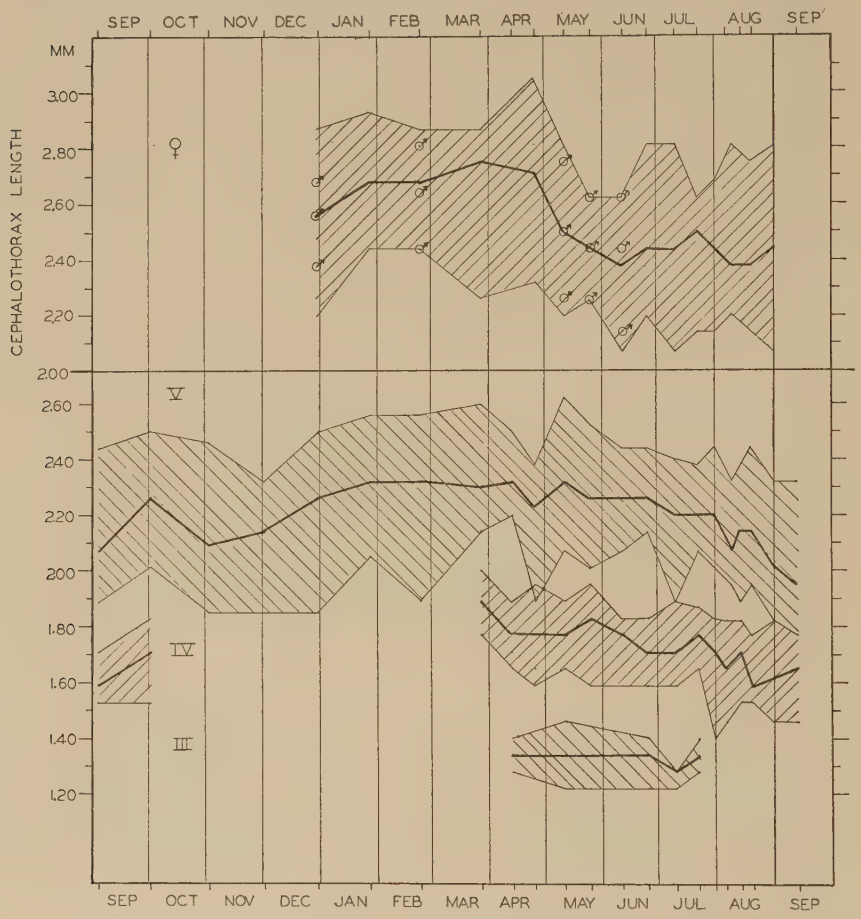

FIG. 7. Cephalothorax length of *Calanus* copepodid stages III, IV, and V and adult ♀ at Station 3 during 1935–6. The shaded area indicates the range and the heavy line the mean of 25 measurements. Since males were sufficiently numerous to measure on only five occasions, the limits of the range and the mean are indicated by the ♂ symbols placed on the upper diagram. It will be noted that the scales of the upper and lower diagrams overlap to a certain extent.

lated for his *Calanus* agrees well with the approximate interval between our spring and summer generations. Marshall, Nicholls, and Orr (1934) found that in the Clyde Sea three generations of *Calanus* occurred during the course of a year. The spawning periods for these

generations took place in March, May, and June. Our observations differ only in that the batches of naupliï appearing off Woods Hole from March to May seemed to belong to the same generation. Bogorov (1934) reports that three generations occur in the Plymouth area. He believes spawning to take place in February–March, May, and intermittently from June to August. Other investigators (Paulsen, 1906; Bigelow, 1926; Farran, 1927; Russell, 1928; Ruud, 1929; and Sømme, 1934) have found a similar succession of two or more generations in their respective areas, but since thorough reviews have been made by Fish (1936) and by Nicholls (1933), their results will not be discussed here.[6]

Variation in Size

The cephalothorax length of 25 specimens of copepodid Stage V was measured for each haul throughout the year and for Stages III and IV and for the adults on those occasions when these groups were sufficiently numerous (Fig. 7). The range of the measurements for each group in each haul was greatest for the adults and progressively less for the younger stages. The average length of Stage V did not fluctuate widely but was found to be somewhat greater from January to May than during the rest of the year. Stage IV similarly diminishes in size after the spring months have been passed. The adult males and females averaged about 2.65 mm. in length from January through April, but in May a sudden drop occurred to about 2.45 mm. and this smaller size persisted through the summer.

The abrupt reduction in the size of the adults in May coincides with the appearance in the hauls of the mature males and females of the new spring generation (Figs. 4 and 5). These individuals were spawned at the end of April or early in May when the temperature ranged between 5° and 9° C. We have already seen that the generation which was produced in June at temperatures of 11° to 15° C. apparently did not reach maturity until the following January or February. Consequently, the summer generation resulted in larger adults than the spring generation although the latter group was spawned at a temperature about 6° C. lower. This relationship with temperature is just the reverse [7] of that reported by Marshall, Nicholls, and Orr (1934) and by Bogorov (1934). These investigators found that the individuals of the spring generation were the largest of the year and Bogorov reported

[6] Results of a similar nature have been reported by Wimpenny (1936) in a publication which appeared since this paper went to press.

[7] The adult females which were taken in April and which were of large size may possibly have been spawned in March and, if so, present a case of correlation of large size and low temperature during the spawning period.

that the females of this generation were 1.2 times larger than those of the autumn-winter generation.

Comparison with Phytoplankton and Nannoplankton

The phytoplankton obtained in the water samples taken at 2, 15, and 30 meters on each occasion has been analyzed by Lillick (1937). She reports that during the summer of 1935 the phytoplankton was dominated first by *Chætoceros* and associated forms and later by *Rhizosolenia*. On October 1 the diatoms reached a maximum.[8] During the rest of the autumn and early winter the phytoplankton was extremely poor. Late in January numbers increased somewhat but by the end of February the phytoplankton was scarce again. On no occasion was a typical spring diatom maximum encountered but Miss Lillick cites evidence for believing that a great flowering of diatoms took place early in February at a time between two visits to the station. During the late spring and summer of 1936 the phytoplankton remained at a low ebb, with *Guinardia* appearing as the dominant form, until August 9 when for a period of four days a flowering of *Rhizosolenia* and *Guinardia* occurred.

Diatoms were the most prominent element of the flora at all times in this region, but dinoflagellates appeared in smaller numbers throughout the year especially in summer and fall. In addition Miss Lillick lays stress upon a group of flagellated and pigmented forms which appeared in all the samples in very large numbers. Although this group was made up entirely of exceedingly small forms, she states that their frequency was so great as to make them significant in the phytoplankton population and she believes that "they must doubtless play an important part in the general food cycle of the region."

Special water samples for the study of the bacterial population were taken by Dr. C. E. Renn at 5-meter intervals from the surface to the bottom on each trip to Station 3 from October 1, 1935 to May 26, 1936. The numbers of cells per cc. as determined by plate counts ranged from 30 to 350 during the first three months but from February to May no counts greater than 33 were obtained (Renn, 1937). Although the actual numbers of bacteria in the sea may have been a thousand times greater than this, we have shown elsewhere that populations of these dimensions cannot be a significant source of food for *Calanus* (Fuller and Clarke, 1936). Besides the bacteria, and the pigmented forms

[8] Our observations on the zoöplankton were not made at sufficiently short intervals to determine conclusively whether or not this flowering coincided exactly with a marked reduction in the number of grazing animals (*cf.* Harvey, Cooper, Lebour, and Russell, 1935). In 1935 a sharp drop in the number of *Calanus* occurred on Nov. 2; in 1936 a similar diminution of numbers took place on August 31.

mentioned above, to which Miss Lillick confined her attention, other nannoplankton types undoubtedly existed—possibly in significant quantities. The presence of great numbers of these, during the summer months at least, has been demonstrated by Lackey (1936). In most routine investigations many of the smaller and more delicate forms are probably overlooked because the usual preservatives destroy them or render them unrecognizable.

Since Marshall, Nicholls, and Orr (1934) found that in Loch Striven the periods of diatom increases coincided with the three main spawning periods of *Calanus*, it is interesting to examine our data for similar correlations. For this purpose observations should have been taken at much shorter intervals than was possible in the present

TABLE III

Phytoplankton at Station 3, March to June, 1936. The number of cells per liter at 2, 15, and 30 meters have been averaged.

	Mar. 27	Apr. 13*	Apr. 25	May 11*	May 25	June 11	June 25
Diatoms	33	9,450	600	4,700	1,467	2,300	700
Dinoflagellates	67	100	1,300	0	67	0	3,767
"Flagellates"	300	5,750	1,433	950	2,633	7,533	6,767
Other forms	0	350	0	0	67	100	167
Total	400	15,650	3,333	5,650	4,234	9,933	11,401
Calanus							
Nauplii	Abundant	Abundant		Abundant			
Copepodid I–III		Abundant		Abundant			Abundant

* Average of two depths only.

investigation. Conclusions are also made difficult in our case because of our lack of information in regard to the state of the fauna and flora in contiguous areas and the effect which horizontal movements of water masses would produce. It is clear, however, that whatever diatom flowering may have occurred in the early spring months between two visits to the station, this could not have served as a food supply for our *Calanus* since nauplii did not appear until March 27. On this date and throughout the ensuing four months diatoms were not abundant. Similarly no production of *Calanus* was observed at the times of the secondary diatom maximum in August or October. The phytoplankton which did exist during the breeding periods of *Calanus* may be studied from Table III. Diatoms were relatively numerous on April 13 and May 11, occasions when nauplii and early copepodites were abundant,

but they were scarce on March 27 when the first nauplii of the season appeared and on June 25 when the early copepodites of the second generation came into prominence. On this latter date dinoflagellates were especially numerous. The forms designated as "flagellates" were abundant throughout this period.

Although our data are not sufficient to allow us to conclude which are the essential food organisms for *Calanus* nor in what quantity they are required, nevertheless we have obtained certain facts which limit the possibilities. We have seen that the spawning periods of *Calanus* occurred at times which did not coincide with diatom maxima. We know from Miss Lillick's analysis that throughout the year the diatoms and dinoflagellates appeared suddenly at intervals of a week or two, flourished for a few days only, and then disappeared again. The "flagellates," on the other hand, although small in size, were found in relatively large numbers on all occasions. If *Calanus* feeds chiefly on diatoms, we must conclude either that the small number of cells always present as a minimum is sufficient for their nutrition, or that the food obtained by the copepods at times of local flowerings can be converted into reserve tissue (e.g. oil) which will tide them over until the next period of diatom abundance. The number of diatoms present between flowerings seems too low to fulfill the nutritive requirements of *Calanus* (Fuller and Clarke, 1936; Fuller, 1937) but further investigations may show this not to be the case. As regards the second possibility, we know that *Calanus*, in the later copepodid and adult stages at least, can live for a week or two without food, but is unable to moult successfully under these conditions (*loc. cit.*). The copepods might thus be able to survive without moulting from flowering to flowering—and this may be the actual situation during the autumn and winter—but rapid growth such as took place from April to July would probably be impossible unless adequate nutriment was continuously available. A third possibility which our present observations suggest is that the nannoplankton is important as food for copepods. The "flagellates" which were found at Station 3 at all times in large numbers would represent only a small amount of substance because of their minute size, but if, as seems likely, these pigmented forms are only a small fraction of the total nannoplankton, the latter may turn out to be significant as a food source.

Summary

1. The seasonal production of zoöplankton, particularly of *Calanus finmarchicus*, was investigated by means of scrim nets and a plankton pump at five stations in the vicinity of Woods Hole during the summer

of 1935 and at one offshore station throughout the ensuing year. Collections of phytoplankton and of nannoplankton and measurements of temperature, salinity, phosphates, nitrates, and illumination were carried out at the same time.

2. The zoöplankton consisted largely of copepods, but medusæ, sagittæ, and, at the stations near shore, larvæ of both benthonic and planktonic forms occurred irregularly. *Sagitta elegans* exhibited four main breeding periods during the year.

3. The numerical analysis of the *Calanus* population revealed the presence of nauplii in significant numbers in March, April, and May, and of early copepodites in April–May and June–July. Stage V was found at all seasons. Adult specimens were relatively scarce at all times, but most abundant in May and June. The species as a whole was reduced to small numbers during the autumn and winter.

4. The pump catches and the net hauls agree in indicating that a short-lived generation of *Calanus* occurs during the spring and that this is followed by a long-lived generation. The latter has its origin in the early summer, passes through the autumn and winter as Stage V, and matures early the following spring to give rise to the next short-lived generation.

5. The measurement of the cephalothorax length of 25 specimens in each stage older than copepodid Stage II showed that the average lengths of the various groups did not fluctuate widely during the year except in the case of the adults which exhibited a sudden drop in size in May.

6. The spawning periods of *Calanus* did not occur at times of diatom maxima, and therefore the two phenomena are not directly related in the present case. In regard to the nourishment of this copepod we must conclude (*a*) that the small number of diatoms always present as a minimum is sufficient, or (*b*) that the animals build up sufficient reserve on occasions of small local flowerings of diatoms, which occur at intervals of a week or two, to tide them over the intervening periods, or (*c*) that "flagellates," which were found continually in large numbers, and other types of nannoplankton are important as a food source.

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RELATIONSHIP OF MINIMUM OXYGEN CONCENTRATION TO DENSITY OF THE WATER COLUMN IN THE WESTERN NORTH ATLANTIC

Contribution No. 118 from the Woods Hole Oceanographic Institution

By

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(With one figure)

In connection with studies of the minimum oxygen concentration in the western North Atlantic the density (σ_t) of the level at which this value occurs was analyzed on the basis of available data from stations where the depth of water was 2000 meters or more[1]). In the region west of the 40th meridian and stretching from the equator to latitude 50° N the observed minimum oxygen value (expressed as cc per liter, generally between depths of 200—900 meters) occurred with densities (σ_t) ranging from 26.95 to 27.41. However, within this region, there appeared to be no well defined regional variation of σ_t at the depth of the observed minimum oxygen value, which suggested that since the minimum oxygen value occurs in the part of the water column where density and oxygen values (and other properties) are rapidly changing with depth[2]), that the scattering of associated σ_t values might be largely the result of random sampling, and it seemed likely that if it was possible to estimate the exact minimum oxygen value of the water column that it would generally be found to occur everywhere in the western North Atlantic basin at approximately the same density surface. Such a supposition seems reasonable in view of the fact that the depletion of oxygen from the water column is the result of biological activity and in order to test its significance the following procedure was used.

The observed σ_t values associated with the observed minimum

[1]) This data was obtained from "Dana", "Meteor", and "Atlantis" stations in the region indicated.

[2]) See: "The minimum oxygen concentration in the western basin of the North Atlantic" by H. R. Seiwell. Papers in Physical Oceanography and Meteorology 5. No. 3 (in press).

oxygen values from 135 oceanographic stations in the western North Atlantic were first grouped into cells having a class interval of 0.04 units of σ_t and the frequency distribution in Table 1 formed. The general form of this table suggests that the data are normal. Referring the frequency distribution to BERNOULLI class marks (0, 1, 2, ... n) the first four moments calculated about the BERNOULLI mean (6.311) are:

$$M_0 = 135.000$$
$$M_1 = 0.000$$
$$M_2 = 1088.966$$
$$M_3 = -264.035$$
$$M_4 = 18545.557$$

Table 1.

σ_t class interval	Mid class value	Frequency	Graduated frequency
26.93—26.96	26.95	1	1.4
26.97—27.00	26.99	4	3.0
27.01—27.04	27.03	10	5.6
27.05—27.08	27.07	12	9.1
27.09—27.12	27.11	13	13.2
27.13—27.16	27.15	13	16.8
27.17—27.20	27.19	14	18.9
27.21—27.24	27.23	18	18.7
27.25—27.28	27.27	17	16.4
27.29—27.32	27.31	12	12.6
27.33—27.36	27.35	12	8.6
27.37—27.40	27.39	7	5.2
27.41—27.44	27.43	2	2.7

Applying the SHEPPARD'S Adjustments to the above moments to correct for the error made in assuming that all the frequencies in the class intervals are concentrated at the mean value the adjusted moments become:

$$\mu_0 = 135.000$$
$$\mu_1 = 0.000$$
$$\mu_2 = 1077.716$$
$$\mu_3 = -264.035$$
$$\mu_4 = 18005.011$$

The standard deviation[1]), σ, is then:

$$\sigma = \sqrt{\mu_2/\mu_0} = 2.825$$

[1]) This is the standard deviation of the data when referred to BERNOULLI class marks; the standard deviation when referred to the class mark in table 2 (mid class values) is: $\sigma = 0.11301$.

and the skewness, S:

$$S = \mu_3/2\,\mu_0\,\sigma^3 = -0.04336$$

indicating a slight skewness to the right. The normal frequency curve best fitting this data is thus:

$$y = 47.788\,e^{0.04336\left(\frac{x-6.311}{2.825}\right)} \frac{1}{\sqrt{2\pi}} e^{-1/2\left(\frac{x-6.311}{2.825}\right)}$$

and is superimposed on a histogram of the observed frequency distribution in fig. 1. The data are next graduated from this normal frequency

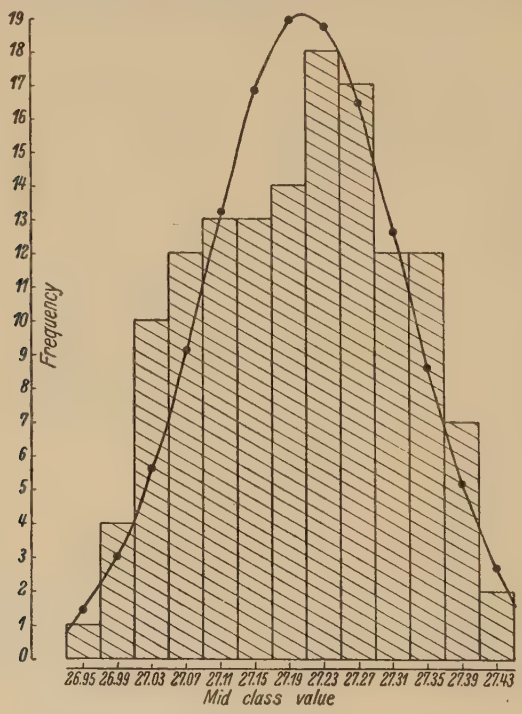

Fig. 1. Frequency distribution of σ_t values at depth of minimum oxygen concentration in the western North Atlantic; observed frequency given by histogram, theoretical frequency fitted by normal curve. See text.

curve and the χ^2 function calculated as a measure of the goodness of fit. Thus:

$$\chi^2 = \frac{(F_1 - f_1)^2}{F_1} + \frac{(F_2 - f_2)^2}{F_2} + \cdots + \frac{(F_n - f_n)^2}{F_n}$$

where F is the theoretical frequency and f the observed frequency. For the particular problem under consideration:

$$\chi^2 = 9.2941$$

since the data are grouped into 13 cells we find the PEARSON probability[1]), P:

$$P = 0.6774.$$

From which it is concluded that in 67.7 times out of 100 we should get in random sampling a fit as bad, or worse than that observed if the real distribution was normal. Thus, we can say that the theoretical curve is a good representation of the distribution of σ_t values associated with the minimum oxygen value (fig. 1).

The ratio:

$$\beta_2 = \mu_4/\mu_0\,\sigma^4 = 2.093$$

and the probable error of

$$\beta_2 = 3.3044/\sqrt{\mu_0} = 0.285.$$

Since for a normal curve $\beta_2 = 3$ we find for the curve under consideration:

$$|\beta_2 - 3| = 0.907$$

which exceeds three times the probable error of β_2 by 0.052, suggesting that the curve may be slightly hypernormal. The difference, however, is too small to be considered significant, and certainly is not sufficiently definite to classify the curve as hypernormal, so for all practical purposes we consider the data as being normal.

The mode (M_0) or the most probable value of σ_t at the minimum oxygen concentration in the western North Atlantic basin is interpolated:

$$M_0 = L + \frac{C\,F}{F+f}$$

where L is the lower limit of the modal class; C, the class interval; F, the frequency of the class above the mode; and, f, the frequency of the class just below the mode. For the problem under consideration:

$$M_0 = 27.232 \pm 0.008.$$

And, since three times the probable error is not likely to be exceeded we tentatively place as the limits of σ_t, between which the minimum oxygen value in the western North Atlantic tends to occur, as:

$$\sigma_t = 27.207 \text{ to } 27.257.$$

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[1]) See: Tables for statisticians and biometricians by KARL PEARSON. Part I, Ed. III, 1930, London.

This result may be tested from the observations at station 2639 (66° 25′ W, 35° 07′ N) where a sampling of the water column was carried out approximately every 20 meters between 730 and 980 meters depth, so that with a high degree of approximation the absolute minimum oxygen value, together with its temperature, salinity, and density was determined. The results in the vicinity of the minimum oxygen value are given in table 2.

Table 2.

Depth	$T°$	$S\,‰$	σ_t	O_2 cc/l
803	11.12	35.39	27.09	3.35
820	10.75	35.39	27.14	3.32
836	10.39	35.31	27.16	3.30
853	9.83	35.28	27.23	3.30
870	9.37	35.21	27.26	3.30
894	8.98	35.17	27.27	3.32
918	8.52	35.15	27.33	3.44

The minimum oxygen value at 853 meters with a σ_t value of 27.23 is in agreement with the theoretical value of 27.232 ± 0.008.

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PUBLICATION SCIENTIFIQUE Nº 4

PHIL E. CHURCH

TEMPERATURES of the WESTERN NORTH ATLANTIC from THERMOGRAPH RECORDS

1937

Secrétariat de l'Association: The University, Liverpool 3

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No. 2. Tidal Bibliography (Third instalment). (1932.)

No. 3. Bibliography on tides and certain kindred matters (Fourth instalment). (1936.)

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Temperatures of the Western North Atlantic from Thermograph Records *

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Commercial vessels with thermographs have made many frequent and rapid crossings of the western part of the North Atlantic from which important surface temperature data have been derived.‡ The first instrument was installed on the S.S. *Coamo*, and has been in continuous operation since 1926. Others were placed in operation later. By November 1928 the number of thermographs carried on vessels provided sufficient data to construct synoptic charts, each of which was made from data taken within a week or, occasionally, ten days. One hundred charts have been constructed from data recorded during the period between November 1928 and December 1933. Approximately twelve hundred thermograms have been studied, and this has extended the period of observation up to the spring of 1935. From the thermograms that have been charted and a study of those not charted, it has been possible to reconstruct

* This study was made under the direction of Dr. H. B. Bigelow, Director of the Woods Hole Oceanographic Institution, and Dr. C. F. Brooks, Director of Blue Hill Observatory, Harvard University. The charts were prepared by Phil E. Church, Keith B. Allan, and E. Monroe Harwood.

† Contribution No. 121 from the Woods Hole Oceanographic Institution.

‡ While this paper was nearing completion, Iselin's (Iselin, 1936) paper on the circulation of the western North Atlantic came off the press. Though these two papers touch the same points in several places, each study has its own set of data, and the subject-matter does not overlap. Iselin's paper treats sub-surface as well as surface conditions from data collected mainly by the *Atlantis*, whereas this paper is concerned only with surface temperatures automatically recorded by vessels running on scheduled trips.

the actual surface temperatures at any time over the western North Atlantic, the changes that occurred from week to week and month to month. Though the period recorded may be considered short, it is probable that the mean temperatures and the annual range, as established by this study, are fairly accurate.

Thirteen thermographs are now operating in eight steamer lanes (see fig. 1). These include (1) Halifax, Boston, Bermuda, and Lesser Antilles ports, and Georgetown (Canadian National S.S. Co.); (2) New York, Cape São Roque, Rio de Janeiro, and Montevideo (São Paulo Tramway, Light, and Power Co., Ltd.); (3) New York to Bermuda (Furness-Bermuda Line); (4) New York to San Juan, P. R. (Puerto Rico Line); (5) New York, Nassau, Miami, and Habana (Munson Line); (6) New York to Habana to Colon (Panama-Pacific Line); (7) Port Tampa to Habana (Peninsula and Occidental Steamship Co.); and (8) Cape São Roque, Trinidad, and New York (São Paulo Tramway, Light, and Power Co., Ltd.).

Up to the beginning of 1931 the vessels plying over Route 1 formerly went from Halifax directly to Bermuda and called at St John, N.B., on the return (route 1 B). Since then they have been rerouted to call at Boston (route 1 A) after leaving Halifax and when returning to Halifax; thus though one important line has been lost an equally valuable data line has been gained.

All these itineraries form a fairly close network of data lines (see fig. 1), particularly in the extra-tropics where surface fluctuations are apt to be rapid. Three lanes within the tropics touch the north coast of South America; one at Cape São Roque, one at Georgetown, and one at Colon. Vessels carrying the thermographs of the São Paulo Tramway, Light, and Power Co., Ltd., bound for New York from Rio de Janeiro, call at Trinidad, thereby producing a data line along the eastern two-thirds of the north coast.

The thermographs (Church, 1932 *a*) are installed with the thermal units exposed to water coming through the intake for the condenser. Though this is not strictly surface water, the intake being from 3 to 8 meters below the surface depending on the vessel and its load, there is little difference between the temperature of the water at that level and the surface (Brooks, 1926; Krummel, 1907). Furthermore, fluctuation from diurnal

heating and nocturnal cooling is practically eliminated at this depth.

Each thermograph is frequently checked against a standard Weather Bureau thermometer by a Weather Bureau official when the vessel is in port at the end or beginning of a voyage. Any error which may creep into the instrument is caught and the thermograph adjusted. Where steamer routes cross and the time interval between vessels is less than a day or two at the point of crossing, or when vessels leave New York within a day, the thermographs may be checked against each other. In only a few instances have they failed to register within ·5 of a degree Centigrade of each other. This checking for accuracy materially aids in establishing that the instrumental errors are well within the limits needed for this study.

Survey of the Temperatures by Sub-areas

A study of the thermograms and the charts show a number of sub-areas of distinct temperature characteristics (see fig. 2). Fixed and exact boundaries cannot be given for each sub-area owing to the mobility of water and the temperature changes during the seasons, but there is a surprising degree of regularity in position of these thermally different surface waters. Furthermore, there is a notable similarity of other physical characteristics in the sub-areas outlined below.

In general, north to south, these sub-areas include: (1) the coastal water; (2) the Slope-water (Harwood and Brooks, 1933; Iselin, 1936); (3) the "cold wall"; (4) the Gulf Stream (Iselin, 1933, 1936); (5) the Central Atlantic water, commonly called the "Sargasso Sea"; and (6) the Northern Equatorial Current. The last named may be further subdivided because of its thermally banded nature.

I. *Coastal Water*

This sub-area includes the water lying over the continental shelf from the Florida Straits to the Gulf of St Lawrence. The seaward limit is definitely marked by the 200-meter contour.

Thermograph records are not suitable for making an accurate study of the surface temperatures of this sub-area

because all lanes, except the Boston-Bermuda, focus at New York. Vessels which make Diamond Shoal Light Vessel (off Cape Hatteras) from New York supply a line of data which is of value for showing only the latitudinal distribution of the isotherms. This must be supplemented by data from other sources to show the direction and distribution of the isotherms over the whole sub-area. Fortunately, detailed descriptions of the surface temperatures exist in the papers of Harwood and Brooks (1933), Bigelow (1928, 1933), Parr (1933), Rathbun (1887), Hachey (1934), and Sandström (1915).

Briefly, the temperatures of this shallow water follow land temperatures more closely than any of the other sub-areas. Thus the annual range is greatest and the time lag of maximum or minimum temperatures from the position of the sun is least. Winter storms stir the water to homogeneous temperatures vertically. In summer a strong thermocline is developed which aids in producing high surface temperatures. South and west of Cape Cod the minimum occurs not later than the last of February. Close inshore the temperature may locally be close to 0° C., but offshore a few miles it is rarely lower than 2° C. and generally higher than 4° C. Seaward, in progressively less shallow water, a regular and rapid increase of surface warmth occurs. Near the shelf-line temperatures are from 6° C. south of Cape Cod to 9° C. off Hatteras. South of Halifax the gradient is less steep, for along the 200-meter contour the temperature is only 3° C. In general, the isotherms closely parallel the shore-line in winter.

At the opposite season the maximum temperatures from Cape Cod to Hatteras are from 21° C. to 27° C., the latter being found at Hatteras. South of Halifax the highest temperatures are between 15° C. and 17° C. At this season the isotherms show a strong tendency to parallel the latitude.

Near Hatteras the annual range is 18° to 20°, off Cape Cod about 17°, and south of Halifax 16° or less.

II. *Slope-water*

The Slope-water occupies the area which separates the "cold wall" of the Gulf Stream and the coastal water. The area fans outward from a point at Cape Hatteras to a width of

140 miles south-east of New York, narrows to approximately 110 miles off Georges Bank, and widens again to an average of about 170 miles off Nova Scotia. The width also depends on the magnitude of the migration of the Gulf Stream, for temporary wanderings of the warm surface water cause an increase or decrease of breadth. The shoreward limit is arbitrarily fixed at the 200-meter line. Seaward from the boundary line the water deepens to more than 2000 meters within a few miles. Coincident with this rapid deepening is an abrupt change of the physical, chemical, and biological characters (Helland-Hansen, 1910) of the water. Furthermore, there is a definite unity in all its properties throughout its whole expanse. Thus, factors other than surface temperature set it apart from its bordering waters.

Annual Cycle of Temperature.—Winter-time charts indicate that the minimum temperatures come in mid-March, nearly a full month later than in the shallow coastal water. At that time the water next the continental shelf is a degree or two higher than the bordering coastal water. The isotherms parallel the continental shelf-line from Nova Scotia south-westward to the bend of New York. The north-eastward trend of the isotherms from this point is suggestive of warmer water mixing with Slope-water, for the latter should be colder than it is at the high latitude. This phenomenon will be explained in fuller detail in the discussion of the Gulf Stream. From the bend at New York the isotherms continue their north-east to south-west course, trending gradually toward the coast. Even so at Cape Hatteras, where this Slope-water ends by tapering to a point, the surface temperature may be as low as 8° C. to 10° C., though in all probability this low temperature represents coastal water which has migrated just over the continental shelf (Iselin, 1936).

The slow rate of warming, after the surface has reached its minimum, until mid-May suggests that winter conditions remain well established for a period of about four months. Harwood and Brooks (1933) have computed the average monthly temperature for the width of the area on the New York-San Juan route and found it to be 13° C. for May, while it averaged 11° C. for the first four months of the year. Winter cooling and the consequent instability of the surface layers, combined with the vigorous stirring by the spring gales, form a deep layer of homo-

geneous temperature. Stability is slow to develop, but once established it is difficult to reverse, and heating proceeds rapidly. The change to summer conditions is rapid, for by mid-July the average is above 22° C. This rise is the result of the abatement of heavy spring weather by mid-May, the increase of insolation, and decreased net radiation (Smithsonian Institution, 1931). Warming continues slowly after summer conditions have become established, and the maximum temperatures arrive about the first week of September, the date of occurrence being governed in a large measure by the prevailing weather conditions. At this time the average near the western edge, adjacent to the 200-meter contour, is about 23° C. to 25° C. As is always true, the edge or transition zone, lying next the coastal water, is somewhat cooler, and the edge lying next the "cold wall" of the Gulf Stream is somewhat warmer, than the average. Between these boundary limits the difference of temperature is small in summer, 2° to 3°, but is large in winter, 5° or more.

Between Halifax and Bermuda, along the northern edge of the Slope-water area, winter minimum temperatures vary between 3° C. and 5° C. Near the "cold wall" the average minimum is considerably higher, 10° C. to 13° C., these high surface temperatures being the result of the large number of warm masses invading that portion of the Slope-water adjacent to the "cold wall," but not present at the continental shelf-line. The table shows the average winter N.-S. gradient off Halifax to be somewhat steeper than across the Slope-water between New York and Bermuda.

Throughout the year there is a very abrupt break in temperature between the coastal and Slope-water at the edge of the continental shelf south of Georges Bank, particularly on the Boston-Bermuda lane.

The average annual range is about 16° for the whole Slope-water area near its western edge, and approximately the same range near the eastern edge south of Halifax. The northern boundary has a greater range between actual extremes, approaching the range of the adjacent coastal water, while that lying close to the "cold wall" has a smaller range.

The mean annual is 16° C. to 17° C. over the western half and a degree or two lower off Halifax.

Slope-Water Temperatures

Location	Winter Minimum	Summer Maximum	Mean Annual	Annual Range	Temperature Gradient per 60 Miles
Close to the 200-meter contour:					
1. Off Hatteras .	8°	25°–26°	17°	17°	
2. Off New York .	7°–9°	23°–24°	15°–16°	16°	
3. Off Halifax .	3°–5°	18°–19°	10°–11°	15°	
Close to the "cold wall":					
1. Off New York .	12°–14°	24°–25°	18°–19°	11°–12°	2·5°
2. Off Halifax .	10°–13°	19°–21°	16°	10°	2·6°–3·0°

Isothermal Patterns.—As a general rule, the isotherms align themselves parallel to the continental shelf, spreading out as the width of the Slope-water area increases. But during the colder months and to a lesser extent during the warmer months, this general pattern is subject to wide changes resulting from the intrusions of warm water, *i.e.* water warmer at the time of these intrusions than the Slope-water. This inflow of warm masses has a great effect on the isothermal pattern at any one time as well as on the thermal conditions of the Slope-water.

Synoptic charts made for each week, or even shorter intervals of time, show the development and life-history of the surface temperatures of these intrusions. A warm mass will appear quite suddenly and spread over a fairly large area with great rapidity. The first indication of the formation of such a mass is a slight spreading of the closely packed isotherms at the "cold wall" and a slight northern bulge in the apparent body of the Gulf Stream. The next observed condition is a more pronounced widening of the Gulf Stream to the east of the initial widening. At this stage the trend of the isotherms shows the mass to be thumblike in shape pointing toward the north-east. The isotherms converge again farther east into a bundle which marks the "cold wall." The pattern is thus indicative of an

eddy or whirl (Church, 1932 *a*, 1932 *b*; Iselin, 1936). Moreover, on the outside edge of this warm mass are irregular fluctuations in temperature, which are suggestive of smaller eddies or whirls, forming on the outer edge of the major whirl. The extent of the major eddy and its distinctness from the rest of the Slope-water is apparent from the sharp temperature gradient around the body of the mass. A southbound vessel passing through one of these masses will encounter three "cold walls"; one on the northern edge of the eddy, another on the southern edge (from higher to lower temperatures), and the "cold wall" adjacent to the Gulf Stream. In such a situation the last "cold wall" does not show as great a temperature contrast as when there is no eddy to the north.

Sources of Warm Masses.—On the charts these warm masses appear as offshoots from the warm water of the Gulf Stream, for they are always located just north of the "cold wall." They have no connection with coastal water. Only rarely do they appear to advance to the continental shelf south of Georges Bank, the narrowest part of the Slope-water sub-area. The surface warmth always greatly exceeds that of the coastal water, even in summer. Their temperatures are above that of the Slope-water, which eliminates any hypothesis that they may be formed of water of that region. The masses are most frequent and best developed during the winter and spring when there is the greatest contrast in surface temperature between the Slope-water and the Gulf Stream. The great frequency and better development (higher temperature) at this time of year, and their location along the northern edge of the Gulf Stream, seems to indicate that they must be of Gulf Stream origin. Moreover, the surface temperatures often indicate that the Gulf Stream is north of its average position as the offshoot forms. This condition appears over a small fraction of the length of the Gulf Stream. The life of each separate mass is not more than a few weeks (Church 1932 *a*). Then this northern offshoot is pinched off by a cold finger, perhaps due to upwelling, and the warmest water (Gulf Stream) is found well to the south.

These warm masses correspond to the "transgressions" of Le Danois (Hachey, 1934, 1936; Iselin, 1936). According to him a "transgression" is "a temporary encroachment of tropical

Atlantic water on water of polar origin." The amount of displacement varies considerably and appears to be a cyclic phenomenon.

Movement of Warm Masses.—These warm masses, after they have been formed, appear to have a very definite movement toward the north-east. A study of the charts made from data taken only a few days apart shows wide changes in the position of the isotherms marking the limits of the warm masses. Abnormally high temperatures occurring intermittently are not suggestive of a current, but if high temperatures are found in one place and not in another nearby at a certain time and the reverse condition is found a little later, it would appear that the warm water had moved from one position to the other. Their disappearance from one place cannot be accounted for by mixing with sub-surface water, for the area each mass occupies is too large, often 150 to 250 miles long, and the return of normal Slope-water temperatures is too rapid. The regularity of progression of high temperatures from west to east indicates movement which generally parallels that of the Gulf Stream. The velocity of the masses is not necessarily constant, though they seem to maintain a fairly constant speed after they are developed. Their velocity, estimated from the time it takes a warm mass to pass a data line, varies from 3 to 10 miles a day.

The initial momentum imparted to each mass and the driving power necessary to maintain its momentum are beyond the scope of this paper. It is quite definitely established, however, that they are not the product of the diverse gales and hurricanes of this region, though the movement of a mass may be accelerated or retarded by these heavy winds. That these masses are not torn from the Gulf Stream and driven by the wind seems evident from the fact that they are most frequent and best developed during the season when the wind is from the north-west quadrant. This wind direction would tend to throw the surface water of the Gulf Stream south into the Central Atlantic sub-area rather than into the Slope-water sub-area (Ekman, 1907, 1923). On the other hand, perhaps the Gulf Stream would have a winter position farther north-west were it not for these gales. However, the north-westerly winds and

gales of the winter and spring in all probability would force surface Slope-water southward and create a pressure tangent to the flow of the Gulf Stream. This could cause a pinching or damming of the Gulf Stream at some point and permit its warm water to move into the Slope-water sub-area. Any loss of water from the Slope-water requires compensating increments from some other bordering sub-area. The only other area, eliminating the Gulf Stream, from which water could come, is the coastal area which is relatively narrow and shallow. Floodings from this area are infrequent and only local in extent, as Bigelow (1933) has shown.

Annual Temperatures.—Owing to the temporary invasions of warm water, this sub-area is characterised by a heterogeneity of temperatures which singularly marks it off from the water of either side. Large monthly and seasonal fluctuations occur along the border adjacent to the Gulf Stream. It is difficult to determine the mean annual temperature, the mean annual range, and the monthly temperatures, because of the intrusions which may be present at one time and absent during another.

The greatest annual range occurs next the boundary of the coastal water. Here, just seaward from the zone of occasional coastal-water intrusions south-east of New York, a representative area, the minima vary between 7° C. and 9° C. (see fig. 5) and occur between the last of January and the middle of March. In the same location the maxima reach 23° C. to 24° C. sometime between the middle of August and the middle of September (see fig. 6). Approximately 16° is the mean annual range.

In winter, when no warm masses invade the sub-area, there is an even steep temperature gradient. At the time of minima temperatures the difference on opposite sides of the sub-area off New York amounts to about 5°. South of Halifax the difference is from 7° to 8°. During the shift from winter to summer conditions this difference is lessened. When summer temperatures have become fully established the amount has shrunk only 2° to 3°. At any season of the year when the Slope-water sub-area is free from warm masses, the isotherms parallel the coast east from the angle of the coast at New York, while to the south they approach and cross the coastal water at an acute angle.

III. *The "Cold Wall"*

The remarkably steep temperature gradient between the Slope-water and the Gulf Stream has long been known as the "cold wall." Though cases of differences as much as 11° within 75 meters can be found in literature, such is not a normal condition. Thermograms do not attest to such extraordinary occurrences. It is true that the records show a sharp contrast within a short distance, but never does the thermograph pen draw a line indicating a nearly instantaneous change. Examination of the records under a magnifying lens shows that it requires from half an hour to a full hour for a vessel to pass through the "cold wall." Such a time-interval indicates a width of 10 to 20 miles as an average. Therefore the temperature change equals about 1° per mile. Most of the vessels cross at right angles to the "cold wall." The average difference, when this zone is best developed (winter), is from 11° to 14°, though occasional records have displayed greater differences.

Not always does the northern edge of the Gulf Stream have this remarkably sharp boundary. Often during the winter the gradient flattens considerably and the change diminishes to 0·2 of a degree or less per mile. This occurs at the time of the movement of a warm mass into the Slope-water sub-area.

Normally during the course of vernal warming as the water to the north increases in temperature, the colder isotherms break off from the "cold wall" and move northward. The water of the "cold wall" then exhibits a progressive diminution of temperature change until there is a difference of only 2° to 4° in late summer when maximum temperatures prevail over the Slope-water and Gulf Stream. Even with this small difference for the "cold wall" the change is abrupt.

Temperatures on the extreme northern edge of the "cold wall" are often a degree or more below those on either side. Sometimes these low temperatures are not matched within 40 to 80 miles to the north (see fig. 7). This cold zone, not more than a mile or two wide, is quite consistent during the colder half-year when the temperature gradient to the north-west is even and regular. The zone is less prominent during the warmer half-year. It has been observed in all months except August. The cold temperature of this zone is obviously the result of upwelling (Church, 1932 *b*).

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IV. *The Gulf Stream*

This well-defined current has long been called any part, or even all, of the great North Atlantic circulation from the Straits of Florida to the northernmost point of the Norwegian coast. Fortunately this chaos is being cleared, in oceanographic circles at least, for the name Gulf Stream is reserved for that portion of the great North Atlantic eddy which is between the north-eastern edge of the Blake Plateau (off the North Carolina coast) and the "tail" of the Grand Banks (Iselin, 1933, 1936).

The location of the lateral edges of the Gulf Stream are not as easily defined nor located. On all steamer crossings used in this study it has been known that the Gulf Stream has made wide temporary excursions from its normal path. These lateral swingings are still unpredictable as to the time when they will start; but once started are rapid in development. A few studies have been devoted to either the course of the main temperature axis (Pillsbury, 1891), or the mean position (U.S. Coast and Geodetic Survey Chart 1007). From the thermograms which have been made it has been possible to draw true boundaries, for the first time, as shown by the temperature and temperature changes of the surface water.

McEwen has pointed out that a current can be detected from a continuous plus or minus temperature departure (McEwen, 1915). Based on this conclusion the Gulf Stream is a permanent feature of the western portion of the North Atlantic. Thermograms at all seasons of the year show it as a distinct and separate narrow ribbon of hot water clearly different in temperature, and thus of origin, from that on either side. (See fig. 7.) Its temperature is always higher than that which lies next to it, even during the summer months.

Width of Gulf Stream.—The Gulf Stream is narrowest where the water of the Florida Current flows off the shallow Blake Plateau to form the Stream. At this point, south-east of Cape Hatteras, surface temperatures show a width of approximately 50 miles. Occasional narrow bands of warm water, seaward from the main body of the Gulf Stream, are probably the last remnants of the so-called Antilles Current and the Northern Equatorial Current which have not as yet become incorporated

in the Gulf Stream or body of the wide Central Atlantic (Sargasso Sea) sub-area. These bands do not properly belong to the Gulf Stream for they are not a permanent characteristic. However, they do account for former statements that the Gulf Stream was 150 miles* wide off Hatteras (Marmer, 1929; Pillsbury, 1891). In the Straits of Florida the average width of the Florida Current, as figured from surface temperatures, is about 42 miles, and this point is more than 700 miles to the south of Cape Hatteras. Thus the surface widening of this rapidly moving current is slow indeed. Off Cape Hatteras some Gulf Stream water spreads over the continental shelf, for Diamond Shoals Light Vessel, anchored in 55 meters of water, reports an average dominant set of the water of 0·4 knot to the north-east (Marmer, 1929).

Eastward 165 miles from the Cape, where vessels on the New York-Puerto Rico route cross the Gulf Stream, the width is about 55 miles, the mean determined from eighty-three charted crossings. These widths were computed by measuring the distance between the lowest temperature on the southern edge and the corresponding temperature on the northern edge. Variations of great magnitude have occurred during the period of observation. Twice it has been less than 30 miles wide and six times has been between 30 and 40 miles. Five times it has been more than 80 miles wide, two of which were in excess of 100 miles.

Vessels on the New York-Bermuda route cross the Gulf Stream approximately 300 miles north-east of Hatteras. At this crossing-point, using data from sixty-five charts, the mean width is about 58 miles. Here its width has never been less than 30 miles, but nine times it was less than 40 miles. In contrast, it was more than 100 miles wide no less than six times. East of the Bermuda lane some 400 miles is the Halifax-Bermuda route. Only eighteen crossings have been charted, but these give an average width of 62 miles. Even with these scant data great variations in width, similar in magnitude to those mentioned above, have occurred.

* Iselin (1936, p. 12) gives 130 miles as the average just north of the Cape. Here he uses a velocity (10 cm. per second) as a criterion. Using this same definition for the Gulf Stream he finds it only slightly wider off Nova Scotia.

Though the Gulf Stream shows variations in width from less than 30 miles to more than 130 miles at each of the steamer lanes, except off Hatteras, there is no simultaneous broadening or narrowing over its whole length. At any one time the Stream may be broad on the New York-Bermuda line, narrow on the New York-Puerto Rico line, and broad again between Halifax and Bermuda. Any other possible combination of narrow and wide places may exist. This widening is the result of warm masses debouching from the Gulf Stream into the cooler water of the Slope sub-area. The charts show that warm masses have broken off at any point along the length of the Gulf Stream from Cape Hatteras to the longitude of Halifax. It is probable that these warm masses have also broken off from the Gulf Stream between Halifax and the "tail" of the Grand Banks.

An analysis of the data on the New York-Puerto Rico route indicates but slight, almost negligible, difference in the average widths for the colder half-year (January to July) as against the warmer half-year (July to January). The latter averaged 54 and the former 56 miles. No other crossings have been analysed, for the data period has been of insufficient length.

Annual Cycle of Temperature.—From west to east over the observed part of the Gulf Stream there is but little temperature difference at any one time. However, such differences as are found are significant, for they represent the relative amount of cooling which it experiences on its eastward journey.

To proceed from the least complex to the most complex condition is the normal method of diagnosis. In discussing the temperature régime it appears less confusing to start with minimum temperatures and proceed through the period of warming to the maxima and then through the period of cooling back to the minima to complete the yearly cycle.

South-east of Cape Hatteras, where the Panama-Pacific vessels cross the Gulf Stream at an acute angle, the lowest readings come during February and early March, with a secondary minimum in April. The lowest average is about 23° C. These do not persist long, for the increasing insolation of the northbound sun, the lessening velocity of the winter-time continental winds, and the higher temperature of the water issuing from the Straits

of Florida all combine to cause rapid vernal warming (Brooks and Fitton, 1930). Minimum figures occur nearly simultaneously along the whole length of the current, but are somewhat lower to the east. Representative temperatures are 22° C. on the New York-Puerto Rico line, 21·8° C. on the New York-Bermuda line, and 20·5° C. on the Halifax-Bermuda line. Thus over this portion of the Gulf Stream's length the temperature is lowered some 2·5° within a distance of about 800 miles. This is comparable to a cooling of 1·5° between the Straits of Florida and Cape Hatteras, approximately 800 miles also, at this time of year.

Spring-time warming is rapid, for by the beginning of June the temperature off Hatteras is nearly 27° C., while farther east 26° C., 25·5° C., and 25° C. are average. Though the increase in temperatures is by no means complete at this time, summer-time conditions may be considered as well established. Warming still continues during the following three months, but owing to the greater net radiation the rate is slower.

Maximum temperatures are manifest by the end of August or early September. At this time we find temperatures from about 29° C. to 29·5° C. at Cape Hatteras to 28° C. south of Halifax. Thus the surface of the Gulf Stream cools about 1° during its journey in the summer as compared with 2·5° in winter. Again this temperature difference compares favourably with the difference observed between the Straits of Florida and Cape Hatteras, for while the latter has a temperature of 29° C. to 29·5° C., the former is 30° C. to 30·5° C., or 1° higher. Summer conditions remain fairly constant until October when autumnal cooling increases in rate. By the middle of October the temperatures are almost exactly those of the first week of June. Decreased insolation, greater net radiation, increased contrast between air and water temperatures, and frequent heavy winds and storms all operate to bring the surface to winter temperatures by the beginning of the year (Brooks, 1932). From that time until the minima are reached cooling is slow.

Annual Range of Temperature.—From the discussion of the annual cycle of temperatures it is apparent that the annual range is small for the high latitude of the Gulf Stream. Owing to this small range, 6° off Cape Hatteras and increasing up to only

8° south of Halifax, it follows that this water must be of tropical origin. Water of the Slope-water sub-area, it will be remembered, has about a 15° range, and, as will be seen later, the adjacent part of the Central Atlantic sub-area has a range greater than that of the Gulf Stream. This eliminates the possibility that surface water of the Stream can come from the surface of either of these other sub-areas.

Gulf Stream Temperatures

Location	Winter Minimum	Summer Maximum	Mean Annual	Mean Annual Range	Width (Nautical Miles)
1. Off Hatteras	23°	29·5°	26°	6·5°	50
2. S.E. of New York	22°	29°	25°	7°	55
3. South of Halifax	20·5°	28°	24°	7·5°	62

Departures from the Average.—From the annual régime, averages for any period can be computed. Then by comparing these averages with those that are found at any analogous period the amount of departure, if any, is shown. Though there have been a number of minor departures, less than a degree, only one large departure has occurred during this period of study. During the fall of 1930 and the following winter, cooling was greater than customary, for the winter minimum off Cape Hatteras was a full degree lower than the average. This minus temperature departure persisted until the summer of 1931 when the opposite condition developed with the surface, attaining a +1° departure as far east as the longitude of Halifax.

Though this is the only marked case of departure, it is indicative of the fact that outstanding anomalies can and do occur even where the annual range is quite small. Surges of water with plus or minus departures have been accounted for by varying trade wind strength (Brooks, 1931) in addition to the effect of atmospheric extremes from North America.

Simultaneously with Gulf Stream departures came departures of the same sign, though not as great in magnitude,

over the western part of the wide Central Atlantic sub-area. It is likely that as the Gulf Stream carries this water of anomalous temperature along its course there will be similar departures along the northern edge of the Central Atlantic with an increasing time lag toward the east. In any event, any persistent cooling weather would influence both at once.

Bands of Warm Water South of the Gulf Stream.—Frequently in the colder half-year, particularly during the two months of lowest temperatures, there may be one, two, or even three narrow bands of warm water which lie close to the southern edge of the Gulf Stream. That these warm bands are not isolated warm masses, comparable to those found in the Slope-water sub-area, is evidenced by their presence over all routes. A series of charts, representing several weeks, shows that they develop slowly and disappear slowly, quite in contrast to the Slope-water warm masses. The temperature of each succeeding band away from the Gulf Stream is progressively lower; the final one having a temperature not more than half a degree higher than that of the Central Atlantic sub-area itself. In general, their temperatures, which set them apart from the Gulf Stream and the Central Atlantic sub-area, decrease toward the east, so that in the longitude of Halifax the bands are poorly defined and infrequent.

The bands are absent during the warmer half-year, or at least not prominent enough to be detected. At this time of year there is but little difference in temperature, 1° to 2°, between the Gulf Stream and the Central Atlantic sub-area.

These bands may be the last remnants, restricted in width, of the wider distinct thermal bands found in the Northern Equatorial Current.

Temporary Migrations of the Gulf Stream.—In its flow from west to east the Gulf Stream is seldom, if ever, in its average position or course. Lateral wanderings occur, which are small and minor, at Cape Hatteras, but increase in magnitude of swing toward the east. At Hatteras the main body of the Gulf Stream flows along the seaward side of the continental shelf. Some of the water apparently floods a portion of the continental shelf, for meanderings of the Gulf Stream alternately place the Diamond Shoal Light Vessel in coastal water and Gulf Stream water.

Owing to the angle at which vessels carrying thermographs cross the Gulf Stream at this point, it is quite impossible to determine accurately the amount of swinging back and forth. It is probable, however, that the meanderings do not greatly exceed 30 or 40 miles.

Beyond the point where the Gulf Stream impinges on the continental shelf, its migrations become more pronounced. This is partly the result of the spreading of the warm water and the detaching of warm masses. Though the latter have at one time or another occupied virtually all of the Slope-water sub-area, much of the area north of the average position of the Gulf Stream cannot rightfully be said to have experienced the presence of the Gulf Stream proper. Due south-east of New York, 300 miles north-east of Cape Hatteras, the average position for the northern edge is approximately 240 miles distant, but it has been within 180 miles. At this steamer crossing the southern edge has been nearly as far north as the mean position of the "cold wall." Migrations of the same magnitude have occurred south of the mean position making the total distance of lateral swinging for the Gulf Stream approximately 120 miles at this data line. Progressively toward the east the migrations assume a greater magnitude. During the short period of record available for the Halifax-Bermuda route the northern edge of the Gulf Stream has been within 230 miles of the coast and as far away as 420 miles, though its average position is about 290 miles. Close approaches of the Gulf Stream in this longitude result mainly from the almost semipermanent character (as long as six weeks) of the warm masses, Gulf Stream water flowing into each for such a period that the surface temperature of the warm mass comes to nearly the same temperatures as the parent mass. When a warm mass becomes detached the main flow of the Gulf Stream continues well to the south.

Not always are the lateral swingings caused by the formation and detaching of warm masses. Frequently in summer, when warm masses are absent or poorly defined, the course swings from its normal position. Even so, the magnitude of these digressions, both winter and summer, is such that there is no indication of a definite seasonal or cyclic shifting, for it is as apt to be as close to the continent in winter as in summer.

V. *Central Atlantic*

South and south-east of the Gulf Stream lies the wide expanse of warm water whose surface temperatures are characterised by greater homogeneity than those of the sub-areas previously discussed. The southern edge is poorly defined if its limit is to be set by surface temperatures alone. In the final analysis, factors other than, and in addition to, temperatures will have to be employed to set its equatorward boundary. For the western part of this sub-area, where it is crossed by the New York-Puerto Rico route, Harwood and Brooks (1933) used the point where there was no further increase of temperature with decrease of latitude as the southern extremity. They found the sub-area to be wider in winter than summer, attributing this to the compensating broadening of the Antilles water by the northerly position of the summer sun. According to them the average width is 828 miles; its summer width (June to September) is 787 miles and its winter width (December to March) is 860 miles. Not only does this sub-area vary in width depending on the seasonal change of the breadth of the Antilles water, but also the variations of the position of the Gulf Stream obviously cause temporary and rapid changes of width.

Farther east, on the New York-Cape São Roque route which crosses this sub-area at an angle, greater fluctuations of width from winter to summer develop. In a previous paper (Church, 1934) I suggested the possibility of using the line of 6° annual range as the mean position for the southern limit. The summer boundary is about 300 miles to the north of this location (approximately 24° N. Lat., 53° W. Long.), the point at which there is no increase in surface temperature with lower latitude. At this time the width of the sub-area is very nearly the same as that farther west; namely, 800 miles. This northward movement of the limit cannot be explained on the basis of an increase in volume of the Northern Equatorial Current, for the change in width is far too great. One possible explanation is the greater heating power of the summer sun which brings the temperature of the surface water of the southern part of the Central Atlantic sub-area up to the warmth of the northern part of the Northern Equatorial Current.

Greater net radiation and lesser insolation in the winter-

time permits the southern edge to migrate far to the south, thus widening it some 600 miles from the summer conditions or to 21° N. Lat. at 52° W. Long. Half-way between this point and the same latitude on the New York-Puerto Rico line, thermograms from the Canadian National Line, between Bermuda and the Lesser Antilles, show a somewhat smaller change from summer to winter widths.

Temperatures.—The annual régime of temperature for this sub-area follows that of the Gulf Stream very closely. Minima occur from late February to late March along that portion which borders the Gulf Stream, and varies between 19° C. and 20° C. south-east of New York. South and south-west of Bermuda there is a gradual increase of temperature to approximately latitude 21° N., the southern limit of this sub-area at this season. Here the temperature is between 25° C. and 26° C., a rise of 5° to 6° from that of the northern edge, 800 to 1000 miles to the north. No appreciable difference of temperature exists along the southern edge between the longitudes of the New York-Puerto Rico and the New York-Cape São Roque routes.

The whole sub-area warms simultaneously in spring and summer owing to the small net radiation and the increasing intensity of the northbound sun. Also, heavy weather is for the most part absent. Conversely in fall and early winter the cooling of the superficial layers occurs without time lag of any portion.

From the minimum of late winter, surface warmth increases slowly and uniformly, interrupted along the northern edge only by the bands of warm water which are occasionally present, until the maximum is reached between the middle of August and the middle of September. Next to the Gulf Stream the temperature increases fully 8° from its winter condition to 27° C. or 28° C. north of Bermuda. Summer maxima are fractionally higher to the west of Bermuda and slightly lower to the east.

South from the Gulf Stream the temperatures increase slightly, and in summer attain their maxima north of Puerto Rico near the 26th parallel. North-east of Puerto Rico, on the Cape São Roque route, the highest temperatures are found in approximately the same latitude. Along this parallel the temperature reaches 29° C. to 30° C. The position of this line

of highest temperatures closely corresponds to the axis of the Azores-Bermuda HIGH, where at this season there is a minimum of wind, and therefore a minimum of surface stirring, the development of a strong thermocline, and a maximum of intense sunshine. This line of maximum temperatures also corresponds to Meyer's line of subtropical convergence (National Research Council, U.S.A., 1930).

South from the high temperature axis the water is only a fraction of a degree to a whole degree cooler, 28·5° C. to 29·5° C., and remains so with unchanged temperature as far south as the latitude of Puerto Rico.

The annual range of the western and northern part of this sub-area is considerably more than that of the Gulf Stream, but the annual range of the southern part of the Central Atlantic is similar to that of the northern end of the Florida Current and the south-western part of the Gulf Stream. Whereas the Gulf Stream has a range of about 6° off Cape Hatteras, the adjacent part of the Central Atlantic has a range of at least 9° to 10° and even more in the extreme western portion. This latter portion, which has the greatest range, is subjected to the cold polar air which flows south-eastward with a high velocity and great frequency from the interior of the continent in the winter and exerts its greatest influence on the water north of Cape Hatteras. South of the summer-time southern edge of this sub-area the annual range diminishes rapidly from approximately 8° to 6° in latitude 23° N. off Puerto Rico, and is the same in latitude 25° N. south-east of Bermuda. At the position of the winter-time southern edge, the annual range has decreased to approximately 5·5°.

Temperature Departures.—As previously mentioned, departures from the normal occur in the western part of this sub-area and are of the same sign and time as those which develop in the Gulf Stream. However, the magnitude of the departures is not as large as those of the warmer water to the west and north, being from one-half to three-fourths as much. Nevertheless there is a strong possibility that these smaller departures, as compared to those of the Gulf Stream, exert a greater influence in producing weather abnormalities along the eastern seaboard of the United States than does the warmer but narrow Gulf Stream. Such a statement is based on the fact that the southern

half of the Central Atlantic sub-area, together with the northern part of the Northern Equatorial Current, constitutes the source area for the tropical Atlantic air masses which move or spread westward to the eastern seaboard and then northward to the latitude of Boston before great changes in the lower layers develop. (Willett, 1933). The time during which the air is in contact with the water of the Central Atlantic sub-area is far greater, thus allowing a greater accumulation of heat, than in passing over the narrow Gulf Stream.

VI. *Northern Equatorial Current*

From the southern boundary of the Central Atlantic sub-area to the north coast of South America and east of the Lesser Antilles is the Northern Equatorial Current. It is the sub-area having the least automatically recorded data with which to work. However, its low latitude results in small temperature changes from month to month and year to year. Thus one complete year of record is of great value and far safer on which to base some conclusions, except departures from the normal, than would be true for any of the other sub-areas. Data are available along two routes in this sub-area: the Cape São Roque line of crossing from New York, and the line between Cape São Roque and Trinidad. Two other lines are of value for this sub-area though both lie just outside the limit: viz. the route from Trinidad northward through the Anegada Passage, and the other from Georgetown, British Guiana, northward following the line of the Lesser Antilles.

At its widest reach (north of Cape São Roque) this sub-area is more than 1500 miles wide. In spite of this great north-south distance, however, there is a striking similarity of surface temperature. An analysis of the thermograms shows at least three belts which are more or less clearly different, resulting from slightly different surface temperatures. In a paper (Church, 1934) I tentatively called them the "northern belt," "central belt," and "equatorial belt." Each of these belts has a somewhat different salinity content and probably other differing physical properties. This is suggestive of somewhat different sources for each of these belts, or a difference of factors which influence the physical properties of each belt.

The Northern Belt.—The northern belt, on the Cape São

Roque route, covers the distance between the southern edge of the Central Atlantic sub-area and approximately 15° N. Lat. The southern edge is not fixed at the latter latitude, but varies from year to year as well as from season to season. It is poorly defined or absent during a large part of the year, but during the winter and spring a sharp change of temperature, from one-half to a whole degree, within 20 to 30 miles, is perhaps sufficient justification for use as a surface temperature boundary. This break in temperature is consistently present each year. The latitude (15° N.) closely coincides with the southern edge of a high salinity (37 parts per M) belt (Iselin, 1936).

Temperatures.—As with the other sub-areas to the north this one has the minimum occurring at least two months behind the position of the sun, for the surface is coolest from late February to late March. Over the northern half (south to approximately 17° N. Lat. at this season) the surface is between 23·4° C. and 24·5° C., and the southern part is between 24·5° C. and 25° C. Warming progresses slowly during the spring and summer, for the maxima are not fully established till September and occasionally as late as early October. During the period of highest temperatures (August through October) the whole belt has about the same surface temperature, *i.e.* 28·5° C. to 29° C., the cooler water generally lying in the southern half. Cooling takes place rather rapidly in late fall and winter to bring the temperatures back to the winter minima to complete the yearly temperature cycle.

Across the western part of this sub-area, viz. along the route north from Trinidad through the Anegada Passage and thence direct to New York, the data show that this belt has narrowed considerably from its great width to the east. Though the summer-time northern edge lies in approximately the same latitude as that on the New York-Cape São Roque route (27° N. Lat.), the winter-time boundary is clearly marked at latitude 22° to 23° N. The southern edge of this belt, distinct in winter and spring only, lies in latitude 17° to 18° N., the latitude of Antigua. The change of temperature which marks this edge does not correspond to the northern end of the chain of the Lesser Antilles. Thus the islands do not effect a temperature change even though the data were taken on the route that lies on the lee-side of the islands. The temperature remains constant

from the north coast of Trinidad to the above-mentioned latitude with no evidence of alteration of warmer and cooler water which might be expected where a line of islands lies athwart a current.

North from the islands in the winter the temperature slowly decreases with increasing latitude. In the summer in this belt the reverse is true, for the water north of latitude 18° N. is fractionally higher than that to the south.

The northern part of the northern belt has a smaller annual range than the contiguous Central Atlantic sub-area. This is the result of the sharp temperature increase, which forms the boundary between these two sub-areas, during the season of minima temperatures. As a result the northern half has an annual range of about 5°. The southern half, owing to higher winter minima, has a range of only 4°. Close to the Antilles, in the western part of this sub-area, the annual range shrinks fractionally to only 3·5°.

The Central Belt.—North-west of Cape São Roque the central belt is set apart from the northern belt by a rapid change of surface warmth in the coldest months similar to the boundary between the Central Atlantic and the northern belt. The belt extends southward from approximately latitude 15° N. to 5° to 7° N., where the annual régime begins to shift from that which normally occurs in the northern hemisphere to a régime showing some, but not all, of the characteristics of the southern hemisphere régime (see fig. 8). The central belt also corresponds to one of homogeneous salinity (36·25 parts per M) (Iselin, 1936), which is less saline than that of the northern belt, but more saline than that of the equatorial belt.

Temperatures.—At no time or place does this belt have a minimum below 25° C. This gives a yearly range of 4° at most, though generally the range is fractionally less, as the maximum in early fall only slightly exceeds 29° C. Obviously this belt should have a lower range than any to the north owing to its lower latitude. Aiding in the production of this small range is the condition of higher minima than the contiguous northern belt. The maxima are slightly lower than the maxima of either the northern belt or the Central Atlantic sub-areas.

South of latitude 16° N., in the longitude of Trinidad, the central belt has contracted to a width of only 360 to 420 miles, due largely to the configuration of the north coast of South

America. Here the central belt occupies all the remaining distance between the latitude of Antigua and the coast of South America. Over this portion of the sub-area the temperatures are very nearly uniform across its entire width at all seasons. The lowest are at the time of year that is normal for the northern hemisphere, February and early March, and average about 26° C., a full degree higher than those north-west of Cape São Roque. The maxima come in early fall, September and early October, and average slightly more than 29° C., the same as those some 700 to 1000 miles to the east. The annual range is less than 4°.

Near Cape São Roque, along the southern edge of this belt, the minimum is produced in February or March. Surface warmth increases slowly but normally until June, at which time a small but noticeable decrease sets in. July averages colder. June, August, September, October, and November are warmer than July. This secondary July minimum is the first indication of the southern hemisphere temperature régime, which makes its initial appearance some 300 to 400 miles north of the equator, north-west of Cape São Roque (see fig. 8).

The Equatorial Belt.—The equatorial belt is considered as all the area south of the central belt. It is widest, therefore, north of Cape São Roque, and tapers to a point near Trinidad. The speed of this portion of the Northern Equatorial Current is rapid, particularly north of the mouth of the Amazon river and off the coast of the Guianas where north-west trends of the coast in reality form constrictions. From supplementary data furnished on the thermograms of the São Paulo Tramway, Light, and Power Co., Ltd., the average speed of the vessels is 395 sea miles in twenty-four hours or an hourly speed of 16·04 knots. Between Cape São Roque and Trinidad the average day's run is 443 sea miles, or an hourly speed of 18·45 knots. Thus along this coast there is an average speed of approximately 2·4 knots. Not infrequently do these vessels, when sailing along the Guiana coast, report a negative propeller slip, or the vessel travelled farther than the propeller, at the unattainable 100 per cent. efficiency, would drive the vessel.

Temperatures.—From the northern boundary south to 2° to 4° N. Lat. the minimum, 27° C. to 27·5° C., is attained in February or March. This is followed by slow warming until

June, at which time a pronounced secondary maximum, 28° C. to 28·5° C., is produced. The following three months are cooler, 27·5° C. to 28° C., than the June maximum, but warmer than the February minimum. The primary maximum is reached in late fall, October and November, the surface warmth then being from 29° C. to 29·5° C. After the maximum has developed the temperatures drop rapidly until the winter minimum is established. The annual range is from 2° to 2·5°.

Between 2° N. Lat. and the equator the annual range is the least of any place in the North Atlantic covered by this paper. The June and November maxima are nearly 28·5° C., and the lowest minimum, which comes in August, is slightly below 27° C. The annual range is thus only 1·5° to 2°.

South of the equator to Cape São Roque the southern hemisphere temperature régime is much clearer than just north of the equator. The February to March minimum has disappeared entirely, but has not yet developed into the maximum, since the greatest warmth occurs from early April to June, the temperature being 28·5° C. (see fig. 8). Cooling brings the surface to lowest temperatures during August and September (26° C. to 26·5° C.). By November the rise in temperature has started and continues until it attains its maximum value in April.

Summary

From thermographs carried by commercial vessels over various routes of the western North Atlantic, enough data have been assembled to make an accurate study of the temperature pattern, the yearly cycle, and the annual range, and also to give an indication of the magnitude of departures. This portion of the Atlantic has a number of sub-areas, each of which is more or less clearly defined from bordering waters by definite surface thermal characters.

The coastal water, covering the continental shelf, has the greatest annual range, amounting to 16° to 20° or more. The minimum comes at the end of February, when close to land the temperature is within a few degrees of 0° C., and an even steep temperature gradient exists out to the 200-meter contour. Summer temperatures vary from 16° C. to 27° C., the latter being found near Cape Hatteras and the former along the Scotian coast.

The Slope-water occupies the area between the coastal

water and the "cold wall." Owing to temporary travelling intrusions of tropical water this sub-area seldom exhibits a regular isothermal pattern. The temperature is coldest next the coastal water and warmest next the "cold wall" at all seasons. The Slope-water has a higher mean annual temperature than the coastal water. The annual range amounts to 10° to 16°, the greater range being nearest the continent.

Of all the sub-areas the "cold wall" has the steepest temperature gradient, averaging from 0·5° to 1·0° per mile. It is seldom less than 10 miles wide and rarely more than 40 miles wide.

The Gulf Stream, seaward from the "cold wall," is a band of hot water which in width averages less than 50 miles off Hatteras and less than 70 miles off Halifax. At times, predominantly in winter, the Stream may widen to double its average width owing to the debouching of warm masses into the Slope-water area. This condition is less frequent in summer. The Stream has an annual range of 7° to 9° between Hatteras and Halifax, and a mean annual averaging about 24° C.

The Central American sub-area extends from the Florida Current and Gulf Stream on the west and north to the Northern Equatorial Current on the south. The annual range is greater than that of the Gulf Stream where the two are contiguous. An even, flat temperature gradient exists over the width of the sub-area in winter, but in summer this condition is present as far south as 27° N. Lat. where the temperature occasionally reaches 30° C. Near the southern edge the annual range is less than 6°. The mean annual temperature is about 25° C.

The Northern Equatorial Current, which occupies the remaining area south to the north coast of South America, has three distinct thermal belts. The northern, whose southern edge is near the 15th parallel, has annual range of approximately 5° or less, and a mean annual of about 27° C. The central belt, less saline than its northern neighbour, has a mean temperature of 27·5° C., and an annual range of 2° to 3°. The equatorial belt, which occupies the remaining distance south from about 5° to 7° N. Lat., displays the first evidence of the southern hemisphere temperature cycle. The annual range is 2° or less, and the mean annual is from 27° C. to 28° C. Near Cape São Roque the maximum arrives during April to June, and the minimum from August to September.

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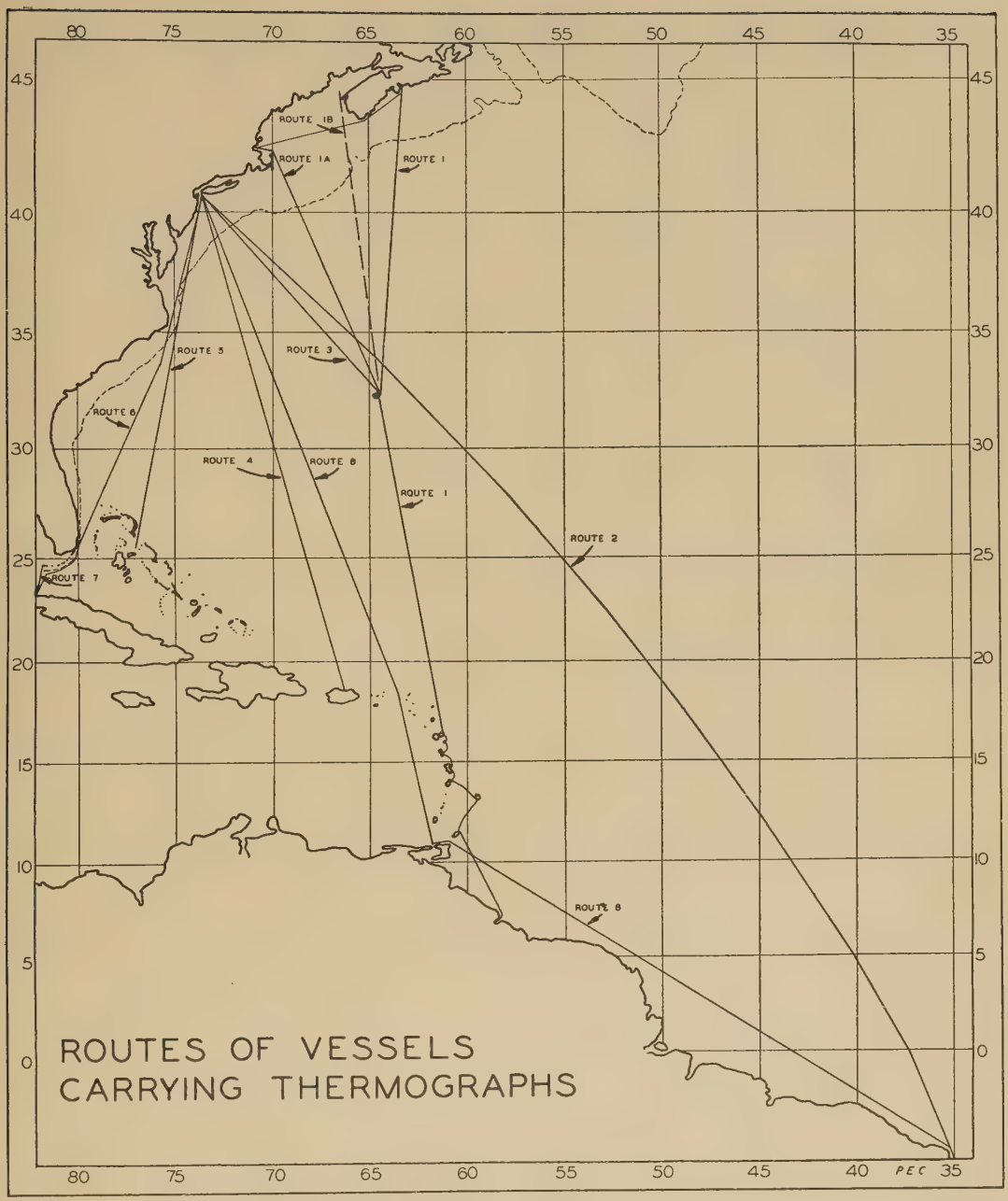
ROUTES OF VESSELS
CARRYING THERMOGRAPHS
ROUTE 1B
ROUTE 1A
ROUTE 1
ROUTE 5
ROUTE 3
ROUTE 6
ROUTE 4
ROUTE 8
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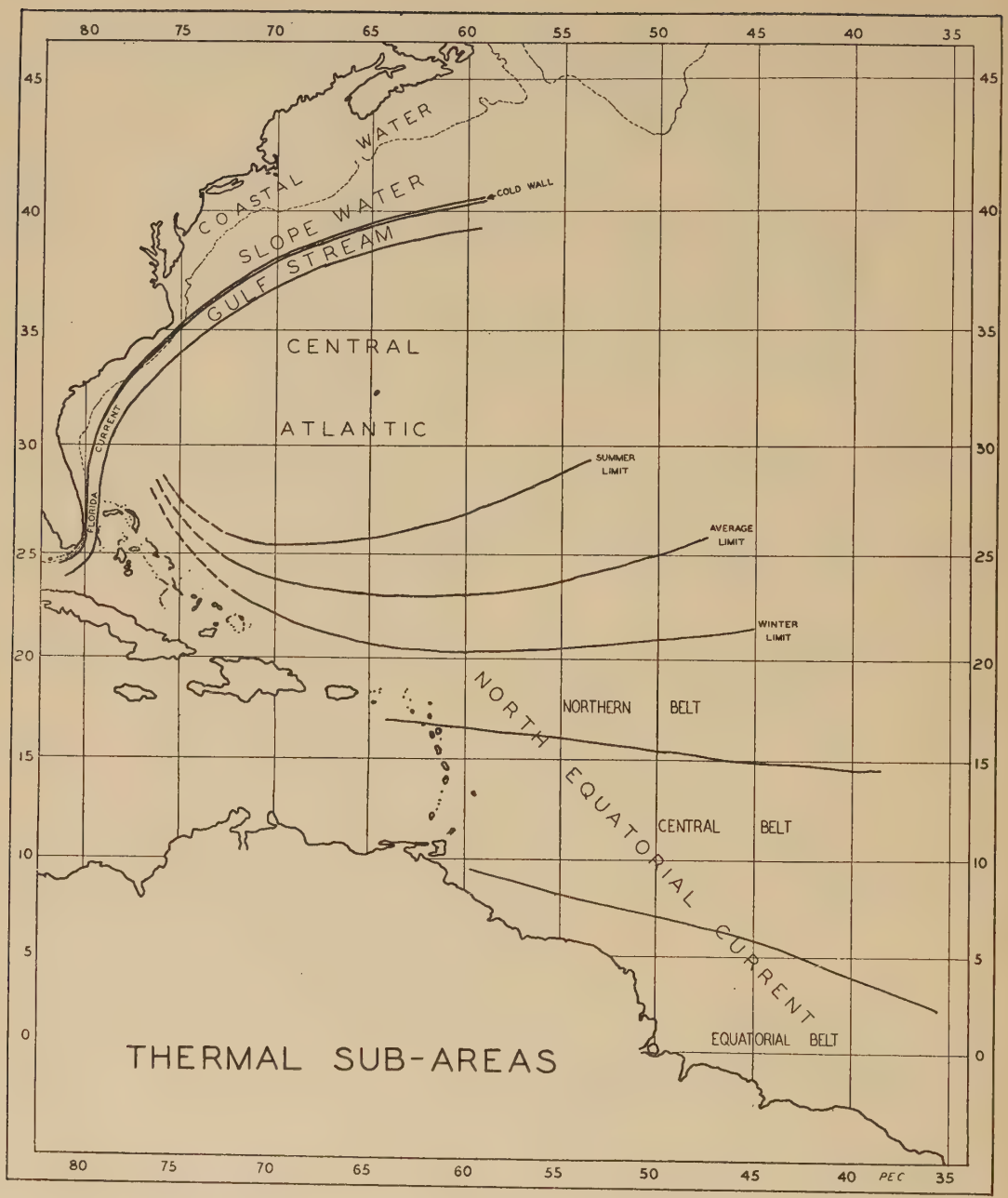
ROUTE 8
80 75 70 65 60 55 50 45 40 35
45 40 35 30 25 20 15 10 5 0

FIG. 1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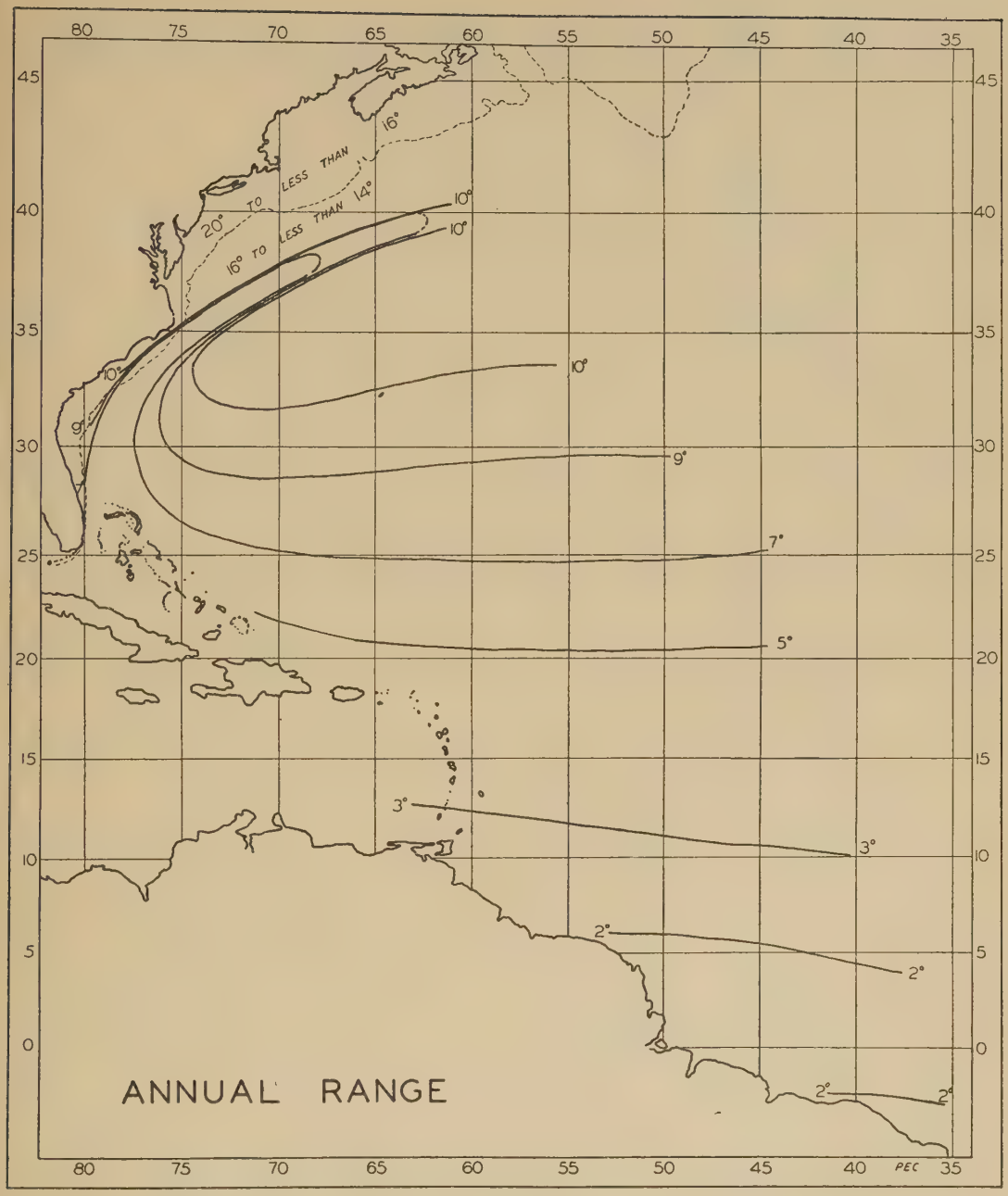
45 40 35 30 25 20 15 10 5 0
COASTAL WATER
SLOPE WATER
GULF STREAM
COLD WALL
CENTRAL
ATLANTIC
FLORIDA CURRENT
SUMMER LIMIT
AVERAGE LIMIT
WINTER LIMIT
NORTH EQUATORIAL CURRENT
NORTHERN BELT
CENTRAL BELT
EQUATORIAL BELT
THERMAL SUB-AREAS
PEC

FIG. 2


80 75 70 65 60 55 50 45 40 35
45 40 35 30 25 20 15 10 5 0
16°
20° TO LESS THAN 16°
16° TO LESS THAN 14°
10°
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10°
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3°
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ANNUAL RANGE
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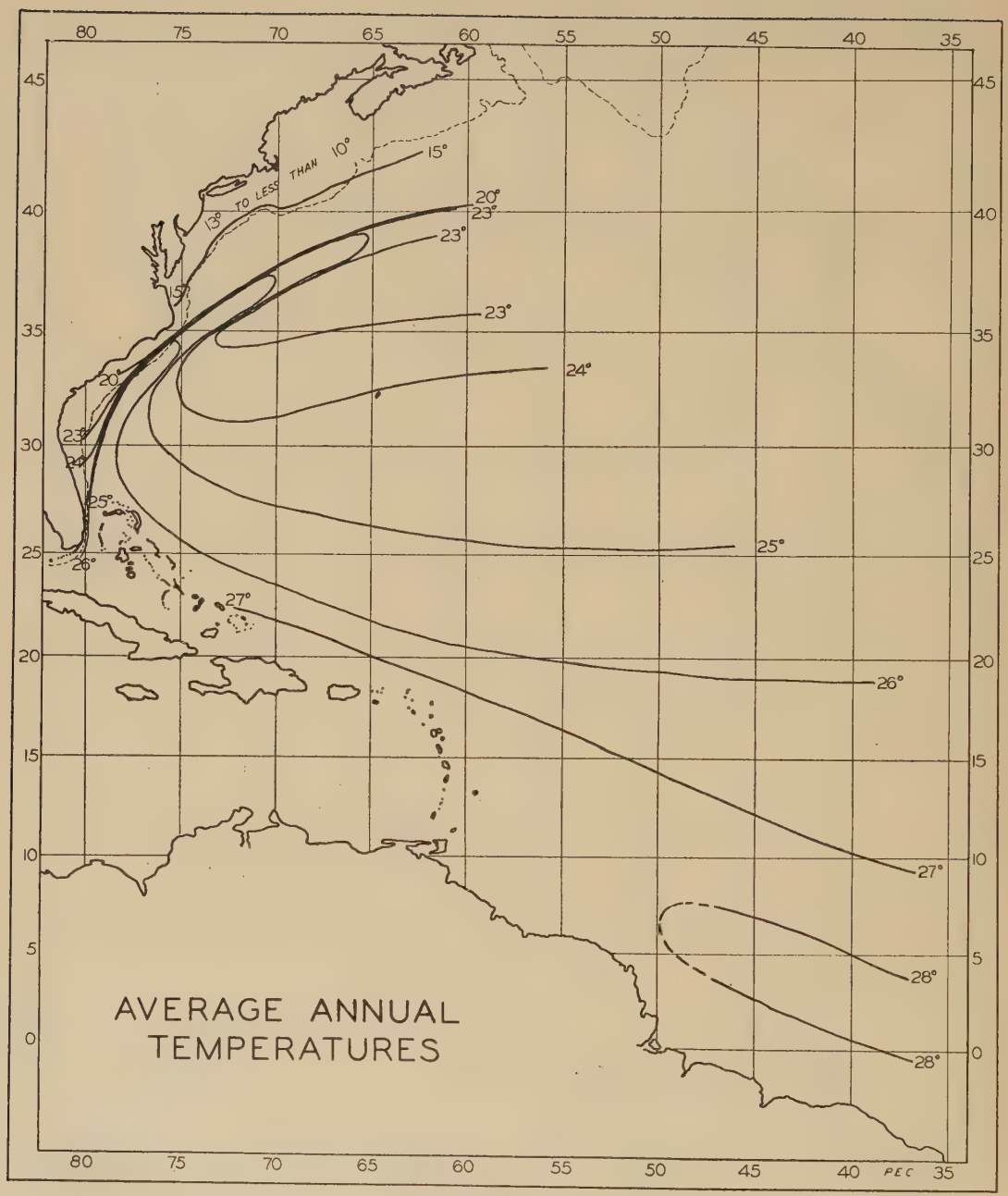
FIG. 3


AVERAGE ANNUAL
TEMPERATURES
80
75
70
65
60
55
50
45
40
35
45
40
35
30
25
20
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0
10°
15°
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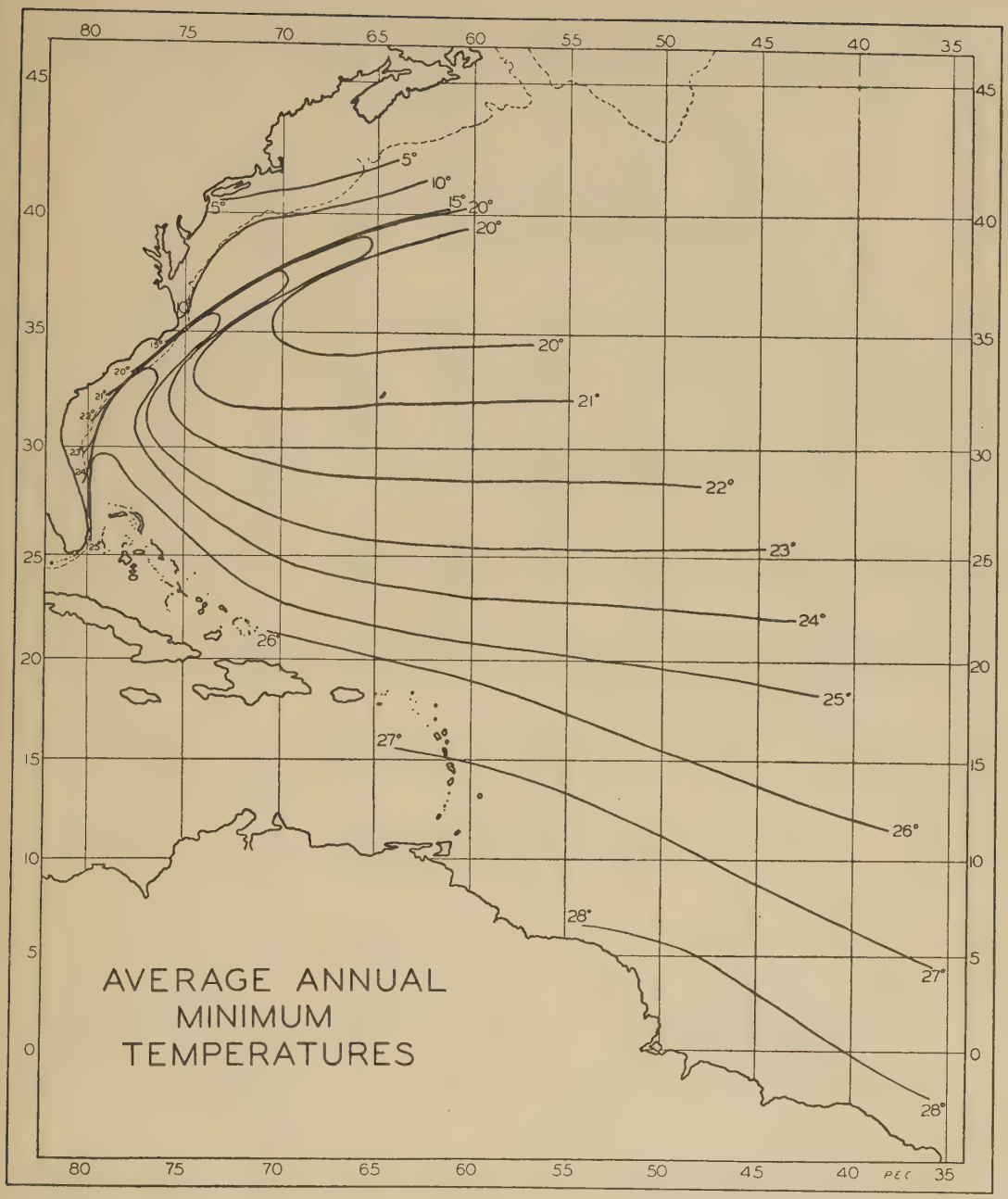
26°
27°
28°

FIG. 4


AVERAGE ANNUAL
MINIMUM
TEMPERATURES
5°
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22°
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25°
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80
75
70
65
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FIG. 5

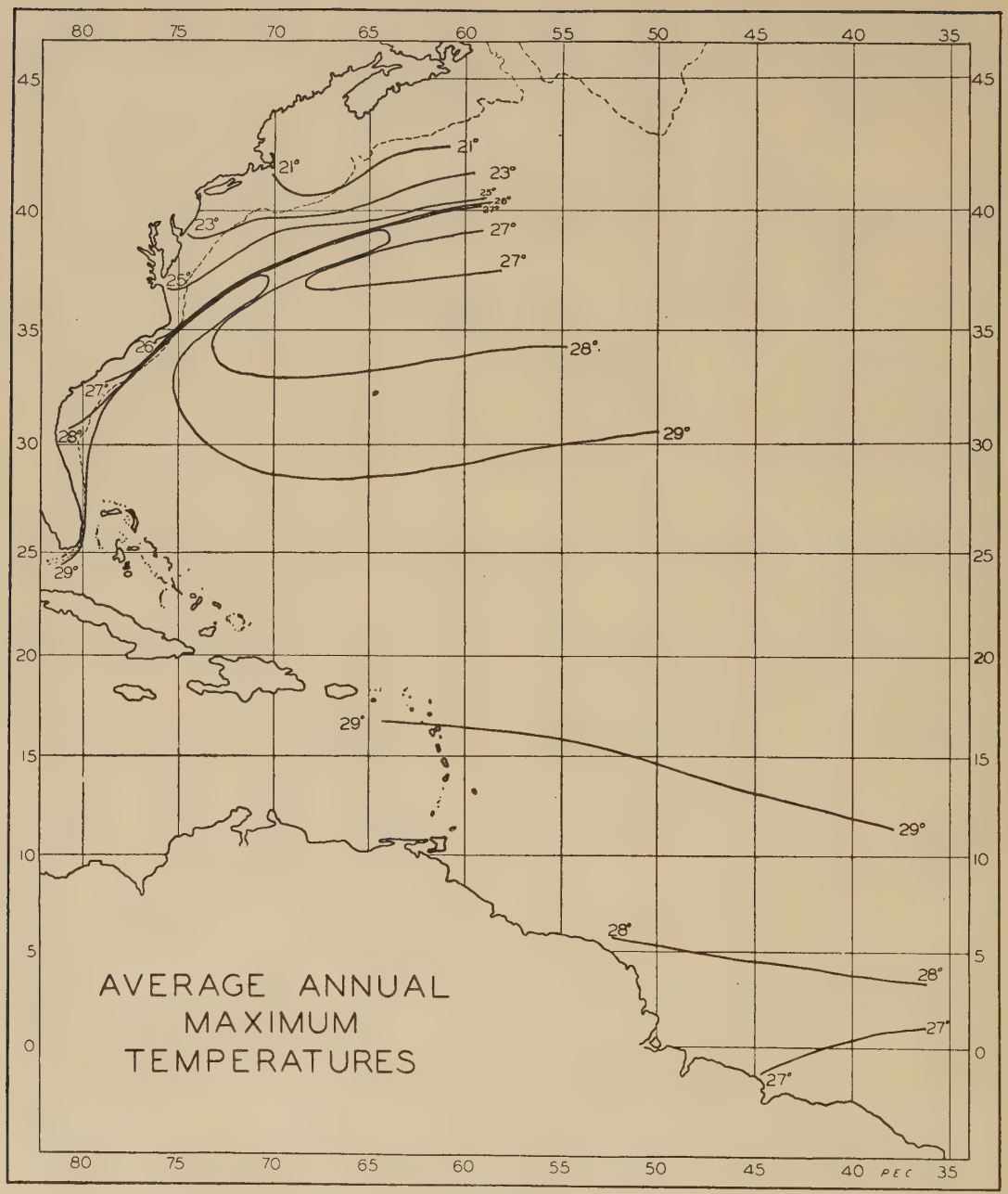
AVERAGE ANNUAL
MAXIMUM
TEMPERATURES
80
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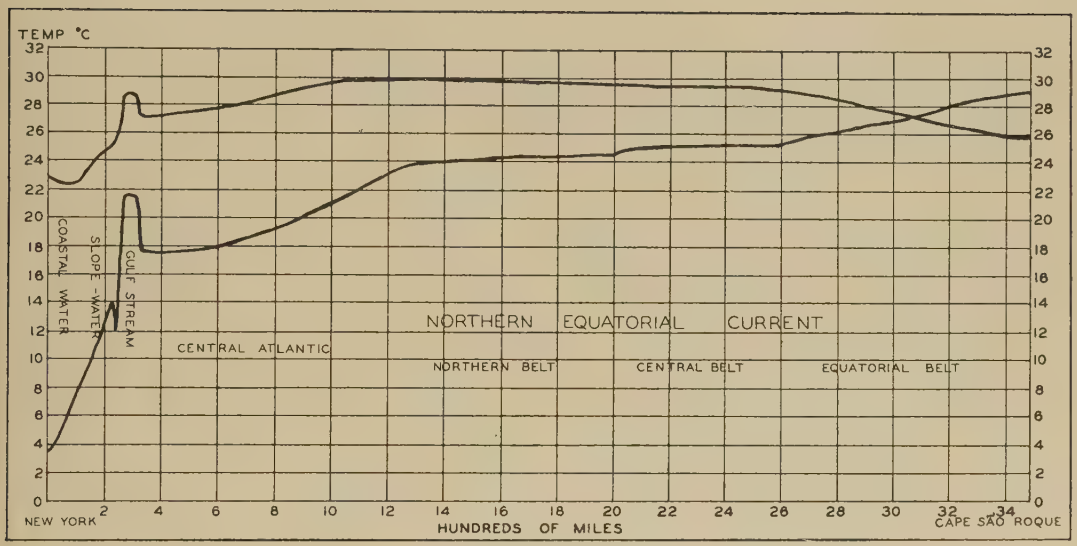
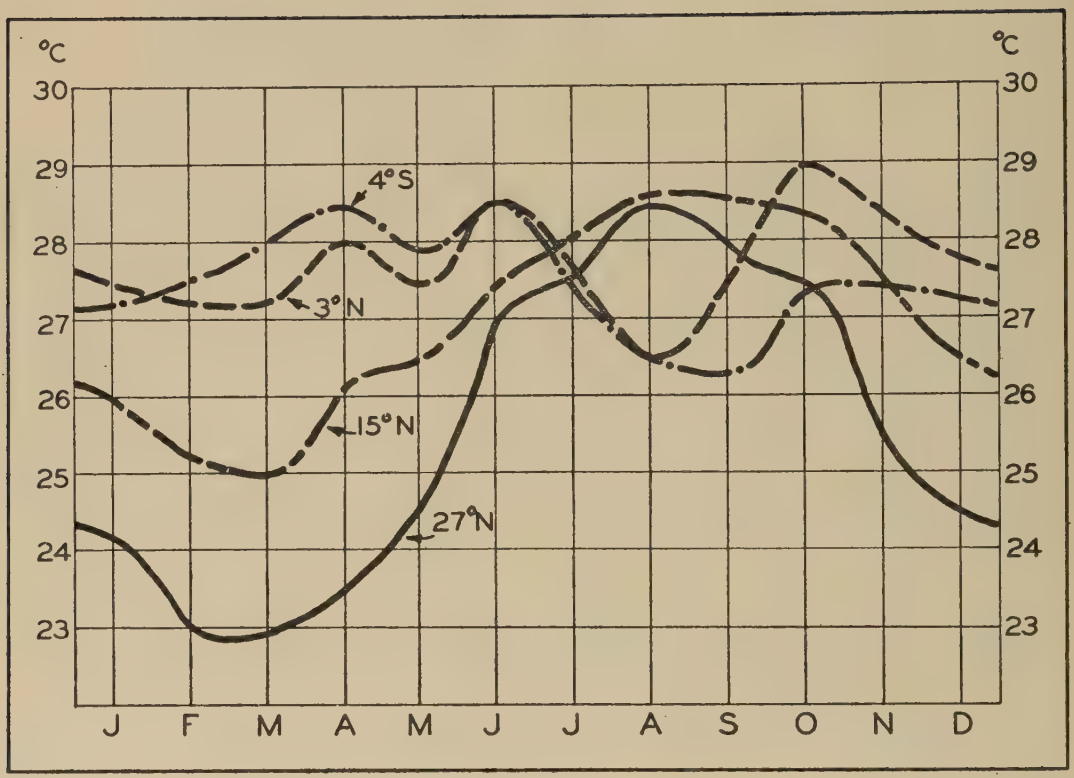
FIG. 6



AVERAGE ANNUAL MAXIMUM AND MINIMUM TEMPERATURES
NEW YORK – CAPE SÃO ROQUE

FIG. 7



YEARLY CYCLE OF TEMPERATURE AT VARIOUS LATITUDES

NEW YORK – CAPE SÃO ROQUE

FIG. 8

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1–6, February, 1937
Printed in U. S. A

OBSERVATIONS UPON THE NITROGEN OF THE PARTICULATE MATTER IN THE SEA [1]

THEODOR VON BRAND

(*From the Woods Hole Oceanographic Institution*)

The present investigation has been undertaken in order to secure data on the amount of organic matter present in particulate form in different regions of the sea. Such information is of importance because in the cycle of life in the sea a very large part of the living matter must occur as nanoplankton. These organisms, together with the more resistant portions of decomposing organisms, detritus, make up the particulate matter which has been studied. Data have accumulated rapidly concerning the dissolved substances such as nitrate, phosphate, etc. which appear in the later stages of the cycle of decomposition but at present almost nothing is known of the quantitative occurrence of these materials while they are bound up in organized matter.

For practical analytical reasons, as well as because of the supreme importance of nitrogenous compounds in the biological cycle, the distribution of particulate matter has been measured in terms of the nitrogen content. Water samples of one to four liters were collected with Nansen bottles and preserved by the addition of 20 cc. of formalin per liter. The particulate matter was concentrated according to the centrifugation method of Steemann-Nielsen and von Brand (1934). The nitrogen content was determined according to von Brand's (1935) modification of Krogh and Keys' (1934) method. In every case duplicate analyses were performed. With a few exceptions, in the case of very low values, they agreed in the range of 10 to 15 per cent. All organisms of about the size of copepods or above were removed. The values obtained thus represent the nitrogen content of the nanoplankton and detritus.

Throughout the whole procedure every care was taken in order to avoid contamination with nitrogen-containing substances. There were

[1] Contribution No. 123 of the Woods Hole Oceanographic Institution.

no indications of any great amount of contamination, but the possibility of a certain degree of contamination cannot be excluded with certainty (for example, from the wire or the closing mechanism of the Nansen bottles). It is not impossible, on the other hand, that during the concentration a certain amount of the particulate matter was lost. The method of concentration gave very satisfactory results with nordic plankton (Steemann-Nielsen and von Brand, 1934); but with Mediterranean plankton considerable losses were reported (Bernard and Fage, 1936). This may, however, be due to slight modifications of technique. Dr. John Fuller (personal communication) tested the method with a diluted culture of *Nitschia closterium*. He compared the values obtained after centrifugation with those calculated from previous direct counts on the undiluted culture. He recovered 94 per cent, whereas Bernard and Fage lost 50 per cent of *Nitschia longissima*.

In Table I are summarized the analytical data from which the results given in Table IV are derived. They demonstrate the order of

TABLE I

Accuracy of the nitrogen method

Water centrifuged for the single analysis in milliliters	Naphthyl red in milliliters						Naphthyl red in milliliters corresp. to 1γ N	γN in particulate matter	
	I. Analysis			II. Analysis				I. Analysis	II. Analysis
	Control precip.	Organ. precip.	Diff.	Control precip.	Organ. precip.	Diff.			
200	2.88	1.30	1.58	2.70	1.00	1.40	0.45	3.5	3.1
100	3.40	2.45	0.95	3.39	2.19	1.20	0.44	2.2	2.7
200	3.27	1.83	1.44	3.31	1.63	1.68	0.44	3.3	3.7
100	2.75	1.34	1.41	2.75	1.46	1.29	0.47	3.0	2.7
100	3.24	1.08	2.16	3.00	0.50	2.50	0.50	4.3	5.0
100	3.18	1.59	1.59	2.96	1.46	1.50	0.45	3.5	3.2
200	3.23	0.65	2.58	3.17	0.32	2.85	0.45	5.7	6.3
200	3.03	0.34	2.69	2.73	0.30	2.43	0.44	6.1	5.5

accuracy which can be expected from the nitrogen method. The percentage error is about the same in most of the data reported in the other tables. The N values actually determined were also in most other cases approximately as high as those shown in Table I. In cases where only small amounts of nitrogen were expected, greater amounts of water were centrifuged (for the single analysis of the deep sea samples usually 1,000–2,000 ml., for those of the Gulf of Maine 200–400 ml.). In some analyses of the deep sea samples with nitrogen values below 1γ N

in the single analysis the percentage error was appreciably higher. The greatest percentage difference observed between two analyses of the same water sample occurred in the 1,300-meter sample of the Sargasso Sea station: I. analysis 0.40γ N, II. analysis 0.85γ N.

Confidence in the quantitative adequacy of the methods employed is also given by a comparison of the results obtained at mid depths in the Gulf of Maine (Table V) with similar estimates of the phosphorus present in particulate form in these waters. Analyses made by Dr. Homer Pyne Smith indicate that about 5γ per liter of PO_4 is present throughout the year in a form which can be separated by filtration. This is one-third the quantity of nitrogen found in particulate form; exactly the ratio to be expected in particles of organic origin.

Results

Table II shows the vertical distribution of the nitrogen in the particulate matter in the Sargasso Sea. The relatively low surface value of 8.4γ per liter is in accordance with the scarcity of plankton in this

Table II

Vertical distribution of the nitrogen of the particulate matter in the Sargasso Sea.
Atlantis Station 2639. Latitude N. 35° 08′. Longitude W. 66° 30′.
July 10–11, 1936.

Depth in meters	Nitrogen γ per liter	Depth in meters	Nitrogen γ per liter	Depth in meters	Nitrogen γ per liter	Depth in meters	Nitrogen γ per liter
0	8.4	500	1.4	1,100	.2	2,000	1.4
50	5.0	600	0	1,200	.2	2,250	2.8
100	3.4	700	.7	1,300	.3	2,500	.5
200	2.3	800	1.1	1,400	1.6	2,750	.8
300	2.0	900	.8	1,600	1.7	3,000	2.3
400	1.4	1,000	1.6	1,800	2.9	4,500–4,750	0

part of the Atlantic. The amount of nitrogen decreases with depth, first rapidly, then more slowly until it is only a fraction of 1γ per liter between 1,100 and 1,300 meters depth. It is apparent that in the deeper layer the values are again somewhat higher. Between 1,400 and 3,000 meters they vary from .5 to 2.8γ per liter. In the deepest sample the nitrogen content was so low that it could not be determined in the particulate matter of the 1.8 liter of water available. The determinations demonstrate that at least in the upper 3,000 meters everywhere particulate organic substance is in suspension. Of course, it cannot be stated that it represents the amount of living substance. It is reasonable to

expect that at least a part is due to the residues of dead organisms or to solid excreta.

A similar series of determinations was secured from the water on the outer slope of Georges Bank (Table III). The distribution of

TABLE III

Vertical distribution of the nitrogen of the particulate matter in the offshore waters.
Latitude N. 40° 20′, Longitude W. 67° 39′. July 24, 1936.
Depth of station, 1,000 meters.

Depths in meters	Nitrogen γ per liter
0	29
50	11
100	7
200	4.7
300	3.6

nitrogen, which shows a progressive decrease from the surface downward to 300 meters, is similar to that occurring at comparable depths in the Sargasso Sea. In the coastal water the nitrogen values are about twice as high as in mid-Atlantic at 50 to 300 meters, and the contrast is even greater at the surface.

A series of determinations has been carried out on surface samples from the region of Georges Bank in order to study the variability in a small area (Table IV). With the exception of the very high value of 47γ N per liter, all figures lie within the range of 18–34γ N per liter.

TABLE IV

Horizontal distribution of the nitrogen of the particulate matter of surface water near Georges Bank.

Date	Position		Nitrogen γ per liter
	Latitude N.	Longitude W.	
July 21, 1936	40° 07′	69° 02′	18
July 21, 1936	40° 09′	69° 04′	24
July 23, 1936	40° 16′	68° 08′	18
July 24, 1936	40° 20′	67° 39′	29
July 25, 1936	41° 21′	66° 07′	47
July 23, 1936	41° 22′	66° 08′	34
July 23, 1936	40° 22′	67° 52′	30
July 26, 1936	40° 27′	67° 42′	29

In the Gulf of Maine water was studied from three deep stations and one shallow station. The results are summarized in Table V. The

distribution of the particulate matter in the upper 40 meters was irregular, but fell very nearly in the range of the values from the surface water near Georges Bank. It is reasonable to assume that the differences found are due to an irregular distribution of the phytoplankton (*cf.* Gran, 1933; Gran and Braarud, 1935). Below 40 meters the conditions in the three deeper stations are on the whole similar. We find at intermediate depths a relatively small amount of particulate matter,

TABLE V

Vertical distribution of the nitrogen of the particulate matter in the Gulf of Maine. Depths not corrected for wire angle.

	Atlantis Station No.			
	2642	2644	2643	2654
Date.....	Aug. 8, 1936	Aug. 18, 1936	Aug. 10, 1936	Aug. 19, 1936
Position....	40° 46′ N. 71° 31′ W.	41° 53′ N. 69° 24′ W.	42° 19′ N. 69° 17′ W.	42° 59′ N. 70° 12′ W.
Depth of station...	64 meters	ca. 200 meters	229 meters	ca. 160 meters
Depth of sample. m.	Nitrogen in γ per liter	Nitrogen in γ per liter	Nitrogen in γ per liter	Nitrogen in γ per liter
0	23	22	12	34
20	25	19	—	29
40	20	28	15	12
60		11	11	10
80		13	10	13
100		11	10	17
120		10	11	—
140		10	17	14
160		11	17	15
180		16	14	
200		16	14	
215			15	

whereas in the deeper layers the amount is always again higher. It should be noticed that both the minima and maxima are within very narrow limits the same at the three stations (9–10 and 16–17γ nitrogen per liter respectively). The differences in the depths at which the minimum and maximum concentrations of nitrogenous particulate matter occur are doubtless due to hydrographic as well as biological causes. Much more information is required before they can profitably be discussed. The striking feature of the waters of the Gulf of Maine in contrast to those from offshore is the higher and more uniform concentration of the particulate matter in the subsurface layers. May this not

be explained by the consideration that in a coastal basin particulate matter cannot sink out of reach of the tidal currents, which extend even to the bottom, and is thus kept more uniformly in suspension?

I should like to acknowledge my indebtedness to Dr. A. C. Redfield, Mr. H. R. Seiwell, Mr. H. C. Stetson and Dr. E. E. Watson for having collected the water samples and to Dr. N. W. Rakestraw for having prepared some of the reagents. The work was done during the tenure of a fellowship granted by the Woods Hole Oceanographic Institution.

Summary

The distribution of nitrogen contained in the particulate matter suspended in the sea has been studied in the Sargasso Sea, on the outer slope of Georges Bank, and in the Gulf of Maine. In the oceanic water the concentration of nitrogenous particulate matter declines sharply with depth to 500 meters and tends to increase slightly below 1,400 meters. On the outer slope of Georges Bank the distribution is similar down to 300 meters, but the concentrations are about twice as great as in mid-ocean at comparable depths. In the Gulf of Maine the nitrogenous particulate matter is more uniformly distributed with respect to depth and is present in greater amounts in the subsurface water than on the outer slope of Georges Bank.

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VIABILITY OF BACTERIA IN SEA WATER[1]

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Woods Hole Oceanographic Institution, New Jersey Agricultural Experiment Station, and New York Medical College and Flower Hospital

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INTRODUCTORY

It has been repeatedly found that the bacterial population in the sea is very limited. This is especially true of sea water in a natural state, although the sea floor, particularly the uppermost surface layer, may contain large numbers of bacteria. Frequently, not more than ten or a dozen bacterial cells are found in 1 cc. of sea water when it is plated out immediately upon a suitable agar or gelatin medium. Close to shore and at certain seasons of the year, this number may reach 500 to 1,000 cells, while far from land it may be as low as 1 or 2 cells per cubic centimeter of sea water. This exceptionally small number of viable cells is not due to a lack of food material in the sea water, since, when the latter is allowed to remain undisturbed in the laboratory for 24 to 72 hours, the number of bacteria capable of developing into colonies on the plate may increase to 50,000 per 1 cc. and even to 10 or 20 times that figure. An appreciable increase may take place even within 2 to 4 hours, or during the period when the sample of sea water is being brought to the laboratory.

Among the explanations suggested for the very low numbers of viable bacteria in natural waters, the following may be mentioned: (1) the presence in sea water of toxic substances which are destructive to bacteria under natural conditions (ZoBell, 1936); (2) the presence of bacteriophage in the water (Arloing *et al.*,

[1] Contribution No. 124 of the Woods Hole Oceanographic Institution; Journal Series Paper of the New Jersey Agricultural Experiment Station, and contribution from New York Medical College and Flower Hospital.

1925); (3) the adsorption of the bacteria by the sea bottom and their sedimentation (Rubentschik *et al.*, 1936); (4) the bactericidal effect of sunlight (Gaarder and Spärck, 1931); (5) the consumption of the bacteria by protozoa and other small animal organisms (Waksman and Carey, 1935); (6) the possible presence in the sea of inactive bacteria which are capable of developing only under more favorable conditions of temperature, aeration and food supply (Korinek, 1927); (7) the lack of sufficient nutriments in the water; (8) the antagonistic relations of other microörganisms; (9) inadequacy of methods commonly used for counting marine bacteria.

Although all of these suggestions may be partly justified, especially under controlled conditions, it is doubtful whether any one of them can explain the phenomena observed in the sea. Most of the investigations, upon which the above explanations rest, were carried out by introducing a pure bacterial culture or a complex natural population into a medium to which it had not been previously accustomed; an example of this is the introduction of typhoid bacteria into sewage or of sewage or river water into sea water.

It has been known since the work of Giaxa (1889) and Miquel (1891) that natural or raw water in which bacteria have grown becomes unfit as a medium for the growth of bacteria, due to the formation of certain soluble and toxic products. Although Greig-Smith (1914) has found that the toxicity is increased by boiling, and ZoBell (1936) has reported that autoclaved and Berkefeld-filtered sea water are also bactericidal, other investigators (Giaxa, 1889) have come to the conclusion that the toxic agents are destroyed by heat.

The following experiments were undertaken in order to obtain further information concerning the survival of bacteria in sea water. Either the undisturbed natural population was used or a culture of a typical marine bacterium was added to the water and its survival determined. An agar-liquefying marine organism, kept in the Culture Collection of the Woods Hole Oceanographic Institution as No. 11, was selected for this purpose; it grew rapidly and the colonies on the plate could easily be distinguished from the majority of other marine bacteria.

EXPERIMENTAL

The first experiment deals with the survival of the marine agar-liquefying bacterium in fresh sea water, in heated sea water and in artificial salt water. It was found that heating of sea water at 80°C., for 30 minutes, was sufficient for sterilization; higher temperatures and pressures were avoided to prevent formation of any toxic substances. The salt water was prepared according to the formula of Allen (1914) and sterilized as above. The sea water for this and subsequent experiments was obtained from Woods Hole Harbor, one hundred or so meters from the dock, filtered through paper and used immediately.

One hundred cubic centimeter quantities of sea water were placed in sterile 250 cc. Erlenmeyer flasks and plugged with cotton. Bacterium No. 11 was grown for 24 hours in a liquid medium containing 1 gram glucose, 1 gram peptone and 0.5 gram K_2HPO_4, in 1,000 cc. sea water. The major reason for using a medium so low in nutrients was to avoid the addition with the inoculum of any appreciable amounts of unused organic compounds to the sea water. The bacterial culture was added in 0.5 and 2.5 cc. amounts to the various flasks of water. These were incubated in the dark at room temperature (18 to 20°C.) and plated out, usually in two dilutions, on an agar medium containing the above nutrients plus 1.5 per cent agar. The plates were incubated for 48 hours and the colonies counted. This period of incubation was found to be sufficient for the development of the agar-liquefying bacterium and for a number of the common sea water bacteria.

The results presented in table 1 show that there was active bacterial multiplication in the fresh and heated sea water, as well as in the prepared salt water. The increase in bacterial numbers may have been due partly to their continued growth at the expense of the small amounts of nutrient material which still remained in the culture inoculum, and partly to a better dispersion of the cells. In the fresh sea water, the bacterial population of the water itself also began to grow rapidly. The maximum numbers were attained in 24 to 48 hours. After that period, the number of bacteria began to diminish rapidly in the

fresh sea water, reaching a minimum in 13 to 29 days. This minimum was comparable to the number of bacteria found in the uninoculated fresh sea water at the same incubation period. The plates showed few colonies of organism No. 11, but numerous colonies of the usual sea water bacteria were present. In the heated water, however, Bacterium No. 11 remained in large numbers up to 13 days and then began to decrease slowly, according to counts made on the 29th day of incubation. Between 29 and 56 days the numbers decreased rapidly. The behavior of the

TABLE 1

Survival of an agar-liquefying marine bacterium in fresh sea water, in sterile sea water, and in prepared salt water

Numbers of bacteria in 1 cc., in thousands

PERIOD OF INCUBATION	TREATMENT OF WATER								
	Untreated fresh sea water			Heated sea water			Salt water		
	Amount of culture No. 11 added								
	None	0.5 cc.	2.5 cc.	None	0.5 cc.	2.5 cc.	None	0.5 cc.	2.5 cc.
Start	1.6	930	4,250	0	2,300	6,250	0	1,470	5,800
1.5 hours	2.3	2,800	19,400	0	3,780	24,800	0	1,690	15,800
4.0 hours	2	4,950	35,600	0	4,600	31,000	0	3,930	24,300
21.5 hours	29	15,100	70,000	0	5,420	23,600	0	3,260	27,400
2 days	120	9,000	56,000	0	9,500	34,000	0	2,700	29,500
4 days	79		688	0	9,150	32,500	0	2,450	27,700
7 days	100	2,140	608		7,900	34,800		2,560	31,000
13 days	52	33.5	25.5		5,300	21,200		2,980	21,500
29 days	25	2.2	29.8		2,650	9,200		700	7,400
56 days	21	39.8	63.4		88	215		105	205

bacteria added to the prepared salt water was very similar to that of the bacteria in the heated sea water.

The results of this experiment have thus brought out definitely the fact that, in fresh sea water, a destructive effect was exerted upon the cells of a marine bacterium added to it. This destruction of the bacteria was usually accompanied by the formation of a very fine coagulum throughout the water, which gradually settled to the bottom of the container.

In order to determine the survival of bacteria in Berkefeld-filtered sea water, a quantity of fresh sea water was filtered

through a Berkefeld of the W type and 100 cc. portions placed in sterile 250 cc. Erlenmeyer flasks. To separate portions of this sea water were added Bacterium No. 11 (1 cc. of a 24-hour-old culture) and sea water 24 hours old (5 cc.). The results presented in table 2 show that the marine bacteria survived readily in Berkefeld-filtered sea water and that no decided injurious effect was observed, even after 14 days incubation.

Passage through a Seitz filter modified the sea water so that the bacteria added to it were rapidly destroyed; only in the case of the larger inoculum was there a gradual adjustment of the organisms to the toxic substances in the sea water. Further

TABLE 2

Survival of marine bacteria in Berkefeld-filtered sea water

Numbers of bacteria in 1 cc., in thousands

PERIOD OF INCUBATION	NATURE OF CULTURE ADDED		
	None	Bacterium 11	Cultured sea water (24 hours old)
Start	0	3,950	0.65
1.5 hours		2,750	0.7
24 hours	0	6,650	1,300
3 days		3,650	6,050
7 days	0	2,850	1,000
14 days	0	5,860	1,060

studies brought out the fact that this destructive effect was largely due to the dissolution of some of the metal in the cup during the long filtration period that was required to collect a large quantity of sea water.

A series of experiments was now carried out for the purpose of establishing the effect of fresh sea water upon both the numbers and activities of marine bacteria. The plate method was used to estimate the number of living cells. As a measure of bacterial activity, oxygen consumption by the Winkler method seemed to be the most sensitive index and it was, therefore, used in these experiments.

Two quantities of water were prepared: (1) fresh sea water, filtered through paper; (2) sea water heated for 30 minutes at

80°C. In order to re-saturate the heated water with oxygen, the flasks containing this water were placed in a refrigerator overnight; the water was then de-saturated by placing the flasks, for a few minutes, in warm water. The oxygen content of the fresh and heated sea water was 5.43 and 5.62 per liter, respectively. Both lots of water were distributed into a series of carefully cleaned and dried 200 cc. oxygen bottles. These were inoculated with varying amounts of a 48-hour culture of Bacterium No. 11. The bottles were incubated under water in the dark and removed at various intervals for the determination of bacterial numbers and oxygen concentration.

The destructive effect of the fresh sea water upon the added bacteria was observed (table 3) within 23 hours incubation; this effect became especially striking after 3 days, when practically all the added bacteria had disappeared. In the heated sea water, however, the bacteria remained at a high level up to nine days. Although the bacteria had been reduced to a minimum in the bottles containing the fresh sea water, there was greater oxygen consumption in these bottles than in those containing the heated sea water, where the added bacteria survived in much greater numbers. The experiment was repeated, with similar results. This could lead to but one conclusion, namely, that the agents responsible for the destruction of the bacterial cells in the fresh sea water were not necessarily destructive to the processes concerned in the decomposition of organic matter in the water, as measured by oxygen consumption. Either these agents themselves consumed the oxygen in the water, or the fewer numbers of bacteria left possessed a much greater power of oxygen consumption (and, therefore, of organic matter decomposition), or a large part of the oxygen consumption was brought about by bacteria which were unable to develop on the agar plate.

In the following experiment, an attempt was made to obtain further information in regard to the relationship between the survival of bacteria in sea water and oxygen consumption, to search for the presence of other organisms in sea water which might modify bacterial activities, and to determine the changes taking place in the water during the early periods after the addi-

tion of the bacteria. All the bottles were sterilized by dry heat, for 18 hours at 60 to 65°C. Several check determinations were made, to eliminate the variability of the individual bottles, which had been frequently obtained in the previous experiments. A

TABLE 3

Survival of an agar-liquefying marine bacterium in fresh and in heated sea water

NATURE OF WATER		FRESH		HEATED	
Incubation	Inoculum added	Bacteria in 1 cc.	Oxygen consumed	Bacteria in 1 cc.	Oxygen consumed
	cc.	*thousands*	*cc. per liter*	*thousands*	*cc. per liter*
3.5 hours	0				
3.5 hours	0.1		0.06	910	0.10
3.5 hours	0.3	1,650	0.09	2,250	0.16
3.5 hours	1.0	5,750	0.39	8,150	0.61
23 hours	0	8.5	0.12	0	0
23 hours	0.1	685	0.66	1,200	0.16
23 hours	0.3			2,335	0.25
23 hours	1.0	3,250	2.16	5,150	0.82
3 days	0				
3 days	0.1	26	0.75	1,490	0.40
3 days	0.3	31	1.66	2,140	0.43
3 days	1.0	6.5	4.38	10,680	2.74
5 days	0	2.8	0.39	50	0.01
5 days	0.1	4.9	0.87	980	0.40
5 days	0.3	5.5	1.74	1,850	0.70
5 days	1.0	7.0	5.16	6,390	2.89
9 days	0				
9 days	0.1	Few		440	0.52
9 days	0.3	4.5	2.40	1,350	0.88
9 days	1.0	5.5	5.43*	5,350	3.58
15 days	0				
15 days	0.1	0.9	1.17	115	0.58
15 days	0.3	1.6	2.46	1,930	1.18
15 days	1.0	2.8	5.43*	1,850	3.88

* Oxygen all used up.

24-hour culture of No. 11 was employed. The results presented in table 4 again confirmed those obtained previously.

In the case of the fresh sea water, the bacterial maximum was obtained within 24 hours, followed by a drop in the number of bacteria. Within 3 days, practically all the added bacteria had

disappeared and were replaced by the native bacterial population of the water, the numbers being of about the same magnitude in the inoculated and uninoculated sea water. The slight difference in favor of the inoculated sea water may possibly be due to the traces of nutrients added with the inoculum. On the other

TABLE 4

Growth and oxygen consumption of a marine bacterium in fresh and heated sea water

NATURE OF WATER		FRESH		HEATED	
Incubation	Inoculum added	Bacteria in 1 cc.	Oxygen consumed	Bacteria in 1 cc.	Oxygen consumed
	cc.	*thousands*	*cc. per liter*	*thousands*	*cc. per liter*
Start	0	2.7	0	0	0
Start	0.3	720	0	500	0
Start	1.0	2,050	0	2,080	0
4 hours	0	4.5	0		
4 hours	0.3	1,260	0.20	2,820	0.36
4 hours	1.0	6,700	0.72	6,500	0.90
9 hours	0	9	0.11	0	0
9 hours	0.3	1,590	0.36	2,990	0.52
9 hours	1.0	6,300	1.01	9,000	1.12
24 hours	0	45	0.23		
24 hours	0.3	3,100	0.95	3,420	0.64
24 hours	1.0	7,100	2.75	12,200	1.41
2 days	0	11	0.45	0.04	0
2 days	0.3	173	1.32	3,800	0.72
2 days	1.0	370	4.16	9,900	1.59
3 days	0	10.5	0.53	62	0.12
3 days	0.3	18*	1.59	3,720	0.78
3 days	1.0	14*	4.71	9,500	1.71
6 days	0	2.4	0.71	2	0.15
6 days	0.3	5.4*	2.09	2,970	1.14
6 days	1.0	18.2*	5.33†	8,800	2.97

* No. 11 practically all disappeared.

† Oxygen all used up.

hand, in the case of the heated sea water, where maximum numbers of bacteria were also obtained in 24 hours, the numbers remained very high even after 6 days incubation, actually 4 to 6 times as high as at the start.

The oxygen consumption in this experiment was similar to that previously found. In the fresh sea water, there was a gradual

disappearance of the oxygen, the rate of its consumption depending on the amount of inoculum added. The greater consumption of the oxygen was due both to the presence of larger numbers of bacterial cells and to greater concentration of the unconsumed nutrients. In practically all cases, the ratio for oxygen consumption in the bottles receiving 0.3 and 1.0 cc. of the inoculum was similar to the ratio of the bacterial numbers in the original inocula. However, after 24 hours incubation, the increasing oxygen consumption was quite independent of the numbers of bacteria since the latter decreased rapidly, while the former, being cumulative, continued to increase. In the heated sea water, the bacterial numbers remained very high even after 6 days incubation, the total number per bottle with 1 cc. inoculum being 1,760,000,000 or four times as great as the number of bacteria originally introduced. The oxygen consumption was still considerably less than that in the fresh sea water.

The water from several of the bottles was centrifuged at the end of the incubation periods and the resulting sediments examined microscopically for the presence of protozoa and other animals. This examination revealed the fact that the heated water contained a large number of bacteria in addition to some dead diatomaceous material. The fresh sea water, on the other hand, contained many protozoa, a number of copepods (12 living forms having been counted in one bottle) and various other lower animal forms.

One may draw from these experiments two broad conclusions, namely, (1) that sea water contains an agent or agents destructive to marine bacteria, and (2) this agent does not interfere with the processes of marine organic matter decomposition, as measured by oxygen consumption. These seemingly contradictory conclusions are possible only by assuming that the agents which are largely responsible for the destruction of the bacteria form a part of the system which is responsible for the decomposition of the organic matter in the sea water. This explanation can help in understanding the reasons for the low bacterial population in natural sea water; the bacterial population is largely held down through the activities of the numerous animals inhabiting the sea.

DISCUSSION

The abundance of bacteria in sea water is controlled by a number of factors, chief among which are (1) the amount and nature of available food material; (2) the rate of bacterial multiplication, leading to the formation of substances injurious to bacterial development; (3) the nature and abundance of the animal population, ranging from minute protozoa to larger forms; (4) the environmental conditions, as exemplified by temperature, and aeration or stagnation of water.

It has been amply demonstrated that extensive bacterial multiplication takes place in sea water, either as a result of (*a*) adding fresh organic matter in the form of algal or of animal residues; (*b*) keeping the water in an undisturbed condition; (*c*) warming the water. Rapid bacterial growth is sooner or later followed by a drop in numbers; the extent of the drop and the equilibrium which is finally established depend on the nature of the stimulus and on the amount of residual organic matter in the water.

The drop in bacterial numbers is greatly delayed and its rate is much slower, when the bacteria are added to sterile sea water instead of to the same water in a fresh state. The bacterial products and the exhaustion of available nutrients cannot, therefore, be alone responsible for the low numbers of bacteria which remain in fresh water in a living and active state. It is believed that another factor, namely the animal population, largely the protozoa and other members of the nannoplankton in the water, is also responsible for bringing about the reduction in the numbers of bacteria. This assumption is substantiated by two facts, first, the multiplication of these organisms in fresh water in which bacterial development has taken place, and secondly, the greater oxygen consumption in the fresh sea water as compared with the sterile sea water, in spite of the greater numbers of bacteria in the latter.

Consumption of oxygen is a measure of the respiratory processes of living systems. When light is excluded, especially in the case of water containing only a limited number of diatoms, the process

of oxygen consumption is carried out by the bacteria and the animal population. The reduction in bacterial numbers accompanied by the growth of animal forms can only mean that the latter are partly responsible for both the destruction of the bacteria and the consumption of the oxygen.

The limited numbers of bacteria under natural conditions in the sea can thus be explained by a state of equilibrium between bacterial multiplication and bacterial destruction. A change in this equilibrium is brought about by a change in food supply, environmental conditions and modification of agents unfavorable to bacteria, whether these are simple organic substances resulting from bacterial metabolism, bacteriolytic substances, bacteriophagic agents, or organisms feeding directly upon the bacteria.

SUMMARY

1. A study has been made of the survival of a marine bacterium added to fresh sea water, to sea water sterilized by heat or by filtration through a Berkefeld filter, and to prepared salt water.

2. The fresh sea water exerted a marked destructive effect upon the cells of the marine bacterium added; this effect followed an initial rise in numbers. Sterilized sea water and prepared salt water had no destructive effect upon the bacteria.

3. The destructive effect of fresh sea water upon the bacteria was not accompanied by a similar effect upon the rate of decomposition of the organic matter in the water, as measured by oxygen consumption.

4. It is suggested that the activities of the animal population of the sea, especially the nannoplankton, can explain, at least partly, both the destruction of the bacteria and the stimulation of the processes of organic matter decomposition.

5. These facts are used as a basis for explaining the low numbers of bacteria usually found in natural sea water.

The authors are indebted to Dr. M. Butler for assistance in making the oxygen determinations.

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A CONTRIBUTION TO THE HYDROGRAPHY OF THE CARIBBEAN AND CAYMAN SEAS

Based upon the Observations made by the Research Ship "Atlantis," 1933–34*

By Albert Eide Parr

Bingham Oceanographic Laboratory

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The opportunity to undertake the investigations here reported upon, and various correlated projects of marine research in the Central American Seas, was created by a generous offer of co-operation from the Woods Hole Oceanographic Institution, by the income from the Bingham Oceanographic Foundation, by a special oceanographic budget granted by Yale University, and by personal contributions from Harry Payne Bingham over and above the income from the Bingham Oceanographic Foundation. To all of these

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Although the special contents of this particular report has been prepared without consultation, the author would nevertheless like to use the occasion to express his gratitude also to Professor C. G. Rossby for encouraging and enlightening discussions on a great many other problems in physical oceanography, which will perhaps not offer equally good opportunity for an adequate expression of this great indebtedness.

INTRODUCTION

The present account is a first report on the continuation of the hydrographic investigations of the Central American Seas begun by the Yale Oceanographic Expedition to the Gulf of Mexico in 1932 (see Parr 1935) and since carried on and extended by a co-operative arrangement between the Woods Hole Oceanographic Institution and the Bingham Oceanographic Foundation of Yale University. The material forming the basis for this report was obtained on the research ship "Atlantis," belonging to the Woods Hole Oceanographic Institution, on two separate occasions, from March 7 to May 5, 1933 and from February 2 to March 4, 1934. Further field work is still in progress and the results will appear in subsequent publications in this series and elsewhere.

MATERIAL AND TREATMENT

The observations were all made in the customary manner, using Nansen reversing bottles and Richter and Wiese thermometers. Unprotected thermometers were used at intervals for accurate determination of depths. The salinity titrations were carried out at the Woods Hole Oceanographic Institution by the routine methods of that laboratory.

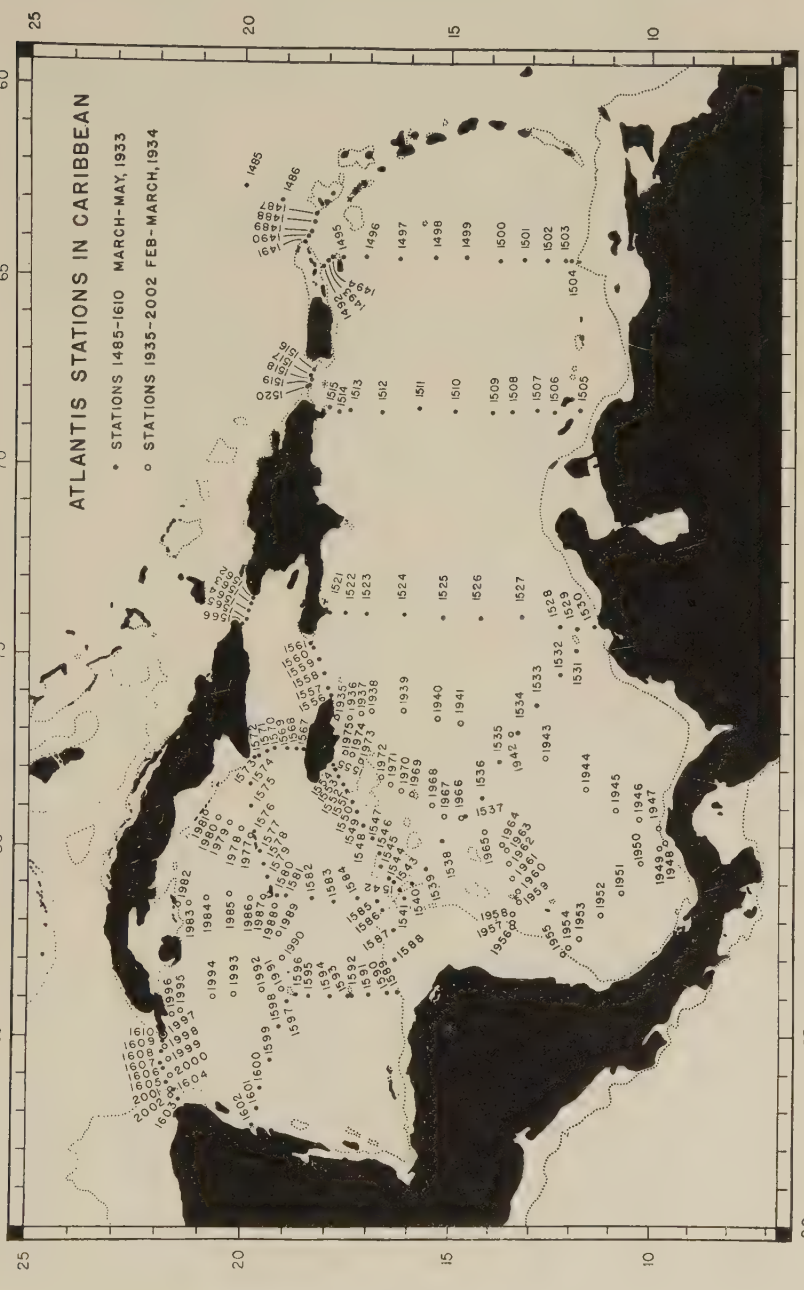

Fig. 1. Atlantis stations in Caribbean and Cayman seas in 1933 and 1934.

			‰				
Salinity at 25 meters − salinity at surface...	+0.10	+0.09	+0.08	+0.07	+0.06	+0.05	+0.04
Number of observations..	1	1+1*	–	1+1*	1	3	4
			‰				
Salinity at 25 meters − salinity at surface...	+0.03	+0.02	+0.01	0.00	−0.01	−0.02	−0.03
Number of observations..	5	5	12	24	5	2	1
	‰						
Salinity at 25 meters − salinity at surface...	−0.04	−0.05					
Number of observations..	1	1	Total observations 67 + 2*				

* Station near shore or in shallow water. 3 additional stations in such localities not included in this table gave +0.24‰; +0.13‰; and −0.23‰.

It was very unfortunate that the hydrographic wire broke, losing a whole string of instruments at a preliminary station immediately preceding the work in the Carribean in 1933. Due to the resulting shortage of deepsea instruments the practice of dipping the surface samples was followed during the remainder of that year's cruise, and has proved to give rather unsatisfactory results. While the surface *temperature* readings are unaffected the surface *salinities* are prevailingly too high to seem credible in comparison with the reliably determined salinities at 25 meters depth. That is, the observations as recorded generally show a slightly but significantly higher density at the surface than at 25 meters depth. It has therefore been necessary to consider the surface salinity observations of 1933 to be unreliable and to regard the salinities determined at 25 meters depth as being representative of the entire surface layer during 1933 in all cases in which these data have been used in critical considerations. That this will not give appreciably misleading results may be seen from the fact that the unreliable surface salinity determinations of 1933 would only in fourteen cases out of 103 produce a change in the grouping of a station in terms of the isotherm intervals plotted in figures 39 and 40, p. 54. It is further demonstrated by the accompanying table of salinity differences between 25 meters depth and surface observed in 1934, which shows an average deviation from 0 of only $0.018^0/_{00}$ for 67 stations not distorted by proximity with topographic obstacles. The table shows only a slight bias in favor of positive deviations in accordance with the general hydrography of the region.

Dynamic depths have been calculated by the simplified method of Sverdrup (1933) using graphical readings for δ_{tp} and δ_{sp} and a more detailed table of Δ_{st} prepared by Mr. Floyd M. Soule, of which the author was permitted to have photostatic copies made.

GEOGRAPHY AND GEOGRAPHICAL NOMENCLATURE OF THE CENTRAL AMERICAN SEAS

The geographical topography of the Central American Seas has been so fully and so well presented by Schuchert (1935) that only a brief synopsis of the region will be required in this report. It would appear that Schuchert in his recent publication, as well as in his earlier works, has been the first investigator to give proper emphasis to the obvious tri-partition of the Central American Seas, and to call adequate attention to the crying need for a separate geographical

Fig. 2. Geography of the Central American sea.

designation for the central basin between the Gulf of Mexico in the northwest, ending at the Yucatan Channel, and the Caribbean proper in the southeast, beginning at the ridge extending from Honduras via Jamaica to Haiti. For this central basin (see figure 2) Schuchert (1929, 1935) has suggested the name Antillean Sea as a designation for the contemporary ocean area, which from the historical geological viewpoint appropriately identifies the region with the geosyncline complementary to the Antillean geanticline. Unfortunately the acceptance of this term in general usage as a designation of the contemporary marine region of the central basin would be likely to prove extremely confusing due to the fact that two-thirds of the Antillean islands are at present in no way connected with the central basin at all, but form a fringe around the Caribbean proper, with which their name as well as their actual location is therefore firmly associated. Use of the term Antillean Sea restricted to the central basin would therefore lead to the confusing result that while the eastern coastal waters of Yucatan would be Antillean, *sensu stricto*, by far the greatest portion of the coastal waters of the Antilles would not be Antillean at all, but Caribbean instead. In loose usage the terms Antillean and Caribbean have already quite reasonably become almost interchangeable.

In view of these insurmountable difficulties confronting the proposed use of the term Antillean Sea as a restricted designation for the central basin, the present writer suggests instead the name *Cayman Sea* for the ocean area representing the contemporary remnant of the Antillean Sea of historical geology, naming the region after the Cayman Islands which occupy the central ridge subdividing the Cayman Sea further into the South Cuban Sea (Schuchert) to the north and the Bartlett Sea to the south. It is to be hoped that this, or some similar unequivocal designation may receive acceptance in geography to end the present difficulty of having only one generally accepted designation (Caribbean) for two entirely distinct ocean basins.

A first report on hydrography of the Gulf of Mexico based upon the results of the Yale oceanographic expedition on the schooner Mabel Taylor in 1932 has already been published (Parr, 1935) and further reports on this area based upon subsequent observations made by the Atlantis is now in preparation. The topography of the Gulf of Mexico is comparatively simple (see figure 3). It includes a large central area of slightly more than 2,000 fathoms depth, and it has two narrow

openings from its southeastern corner. The Straits of Florida has a narrowest width of about 45 nautical miles, and a threshold depth in its northeast portion of less than 500 (less than 400?) fathoms. The Yucatan channel, connecting with the Cayman Sea, is about a hundred miles wide, and has a threshold depth of about 1000–1100 fathoms.

The Cayman Sea is the topographically most complex of the three basins, with a chain of islands and banks (Cayman Brac, Grand Cayman, and Misteriosa Bank) rising from the submarine ridge extending in a westerly direction from the southwest point of Cuba. Midway between Misteriosa Bank and the northern coastal bank of Honduras the tiny Swan Island rises to the surface. Immediately south of the ridge from Cuba to Misteriosa Bank we find the greatest depth of all Central American basins in the long and narrow Bartlett Deep, where soundings over 3400 fathoms depth have been made. The Cayman Sea connects with the open Atlantic, via the Bahaman waters, through the Windward Passage, about 45 miles wide and with a threshold depth of about a 1000–1100 fathoms. It is separated from the Carribean, *sensu stricto*, by the complex system of banks and passages on the ridge between Honduras and Jamaica, where the threshold depth is probably less than 700 fathoms, and by the 105 miles long continuation of this ridge in the passage between Jamaica and the extreme southeast point of Haiti, where the threshold depth would appear to be about 800–1000 fathoms, its exact level being rather uncertain in this region due to inadequate soundings.

The Caribbean, *sensu stricto*, is again of comparatively simple topography except in the proximity of the Honduras-Jamaica ridge, where several deep gullies and islands or banks occur. Farther east there is a slight elevation of the bottom tapering off in a southwesterly direction from the western part of Haiti; and in the extreme east a still higher elevation extends directly south from the eastern bank of the Anegada Passage, reaching to the surface at the minute Aves Island. Otherwise the Caribbean includes a large area of depths between 2000 and 2800 fathoms, of quite simple topography so far as known. The Caribbean opens to the Atlantic in the north only by the shallow Mona Passage between Haiti and Porto Rico, about 60 miles wide and of only about 300 fathoms threshold depth. Its widest single entrance is through the Anegada Passage in the extreme northeast corner, about 55 miles wide and of about 1000–1100 fathoms threshold depth; but some of the passages among the Lesser Antilles,

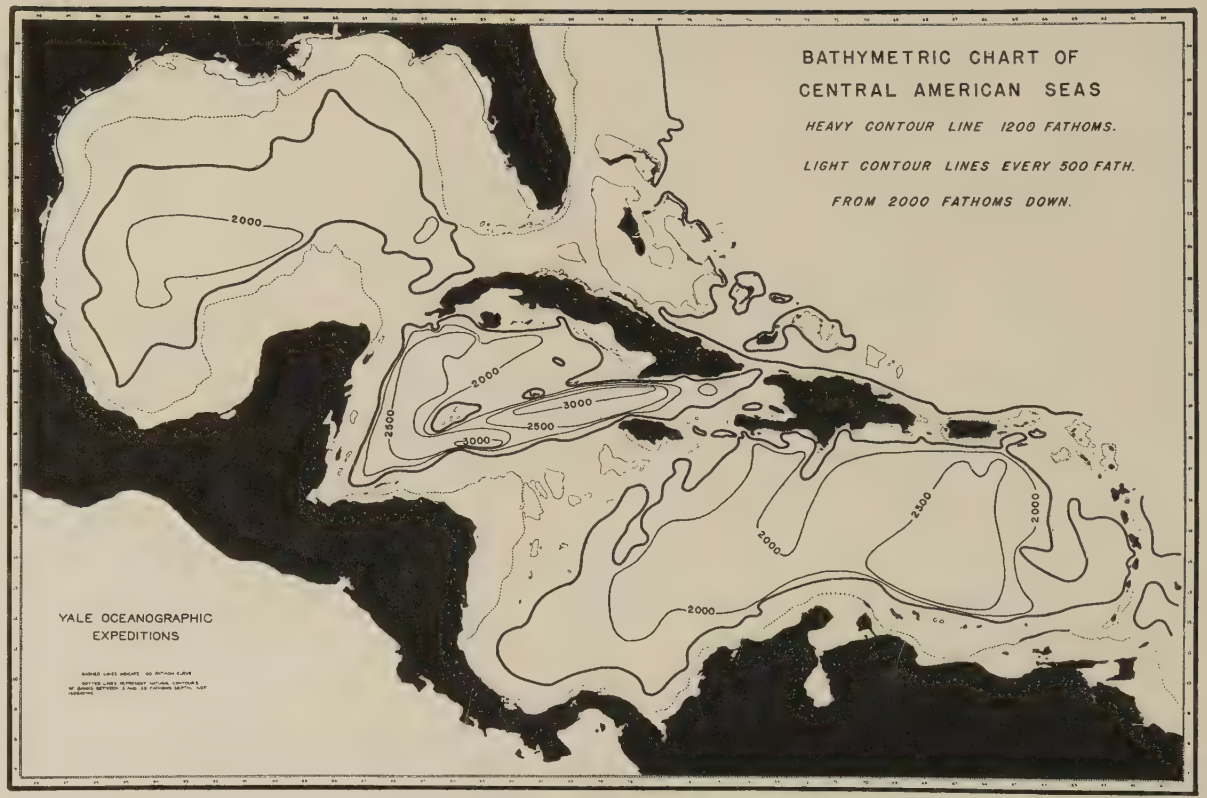

Fig. 3. Bottom topography of the Central American seas. Heavy contour line for 1200 fathoms. Light contour lines for 2000 fathoms and every 500 fathoms below.

particularly between Dominica and Martinique, although narrower, would appear to have about the same threshold depth as the Anegada Passage.

HYDROGRAPHY

Organization of the Hydrographic Report

In the presentation of the hydrography of a region it seems most convenient to begin with an orientation in the general features of vertical and of horizontal distributions. Since a discussion of the origins and relationships of the various water-masses identified by their temperature salinity correlations also requires reference to the general circulation system it furthermore seems advisable to precede the discussion of temperature salinity correlations with a general outline of the main features of dynamic topography. On the basis of these considerations the various aspects of Central American hydrography to be dealt with in this report will be arranged in the following order: (1) Vertical distributions. (2) Horizontal distributions. (3) Dynamic topographies. (4) Temperature salinity correlations, with a discussion of origins and relationships.

The primary tables of observations on which this report is based are being published in the Bulletin Hydrographique of the Conseil International Pour l'Exploration de la Mer (1934 and following years). But since these tables are published in advance they can naturally not be corrected for errors which only become apparent in the final analysis of the data, and they are therefore not always representative of the figures used, or discarded, in the course of this investigation.

VERTICAL DISTRIBUTIONS

In vertical distributions as in all other aspects of Caribbean hydrography we recognize a general fundamental pattern valid for the entire region, and local modifications which in turn may form a regular subordinate pattern or may occur irregularly. The general features can best be learned from a study of selected individual or average vertical curves, while the arrangement of local modifications will appear in the vertical profiles (figs. 5–34) and in the horizontal distribution of thickness and depth of definite layers or surfaces.

General Features

The general pattern of vertical distribution of salinities is shown by some selected examples and averages in fig. 4. The outstanding features are the relatively low salinities at the surface (36.0–36.2‰) increasing sharply to a high maximum (36.5–36.7‰) around 150–200 meters depth, dropping again to a minimum (about 34.78–34.92‰) around 800 meters depth, and finally rising slightly to about 34.96–35.00‰ in the bottom waters. Due to the transverse slope of the entire system the depths of the curves, particularly below the salinity maximum layer, are generally greater on the right side of the main flow, that is in the North and East, than on the left (South and West). This is illustrated in our figure by a comparison between a northern (St. 1521–24) and southern (St. 1526–30) group of stations in our third transverse profile which runs approximately through the middle of the Caribbean Sea (Haiti to Colombia). In the southern group of stations (1526–30) the slope of the water layers has brought the salinity maximum so close to the surface that the normal surface minimum has been virtually obliterated. The greatest average depths for the entire Central American seas are found in the Yucatan Channel as shown by our curve for Stations 1605–1610, the curve for St. 1605, which is conspicuously higher than the average for the profile, being also shown separately.

From a comparison with the average salinity curves for Jacobsen's two areas of the Atlantic North Equatorial region (VI and XIV, Jacobsen 1929), which have also been entered in our figure, we now see that the entire range of variations in vertical distributions in the Caribbean falls within the area in our diagram outlined by these two North Equatorial curves, that is, the North Equatorial vertical distribution pattern persists throughout the Central American Seas and no approach to the entirely distinct vertical pattern of the Sargasso Sea (Jacobsen's area XX) develops in these waters.

Vertical Profiles

The vertical profiles for temperatures and salinities in all Atlantis sections through the Caribbean and the Cayman seas and across their entrances are shown in detail figures 5–34. These illustrations are generally so arranged that the reader must imagine himself facing with the main flow of water through the Central American seas.

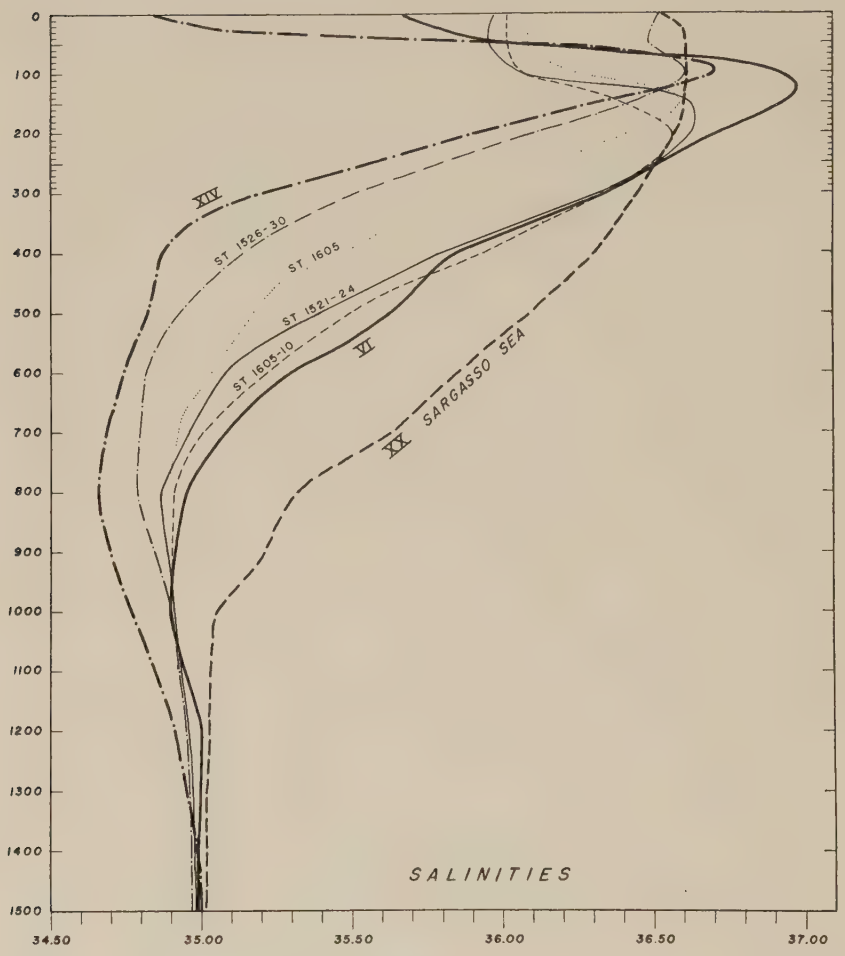

Fig. 4. Vertical salinity curves for Atlantis stations in the Caribbean and Cayman seas compared with average curves for Jacobsen's areas VI, XIV, XX (Sargasso Sea). See text

That is to say the right hand side of the main current (North and East) is also at the right in these figures.

Exceptions from this rule are only found in the case of the profiles through the northern passages (figures 11, 12 and 23–24) and some other sections (figures 13–16) in which placing the right side of the direction of main flow at the right of the illustrations would require a reversal of geographical directions, placing East to the left. Geographical directions are in all cases indicated by large letters above each profile. In view of the uniformity of the deeper layers which makes it difficult to determine the exact depth of the isotherms and isohalines the profiles have only been drawn for the upper 800–1000 meters.

The North-South profiles through the Caribbean (figures 5–10) show fairly uniform slopes resulting in somewhat higher salinities and lower temperatures at the surface and in the upper levels in the South than in the North. In the two northern entrances (Anegada and Mona passages, figures 11 and 12) to the region covered by the three North-South profiles, however, no appreciable slope is visible.

In the Southeast-Northwest profile of 1933, from Colombia to Honduras (figures 13–14) the slope is also from higher levels in Southeast to lower in the Northwest, but this profile cuts tangentially along the direction of the main current and therefore can not be directly interpreted in relation to the flow. Our next profile (figures 15–16) from Panama to Costa Rica cuts diagonally across a major eddy and show a rise of isohalines and isotherms in the middle.

The 1934, Northeast-Southwest profile from Jamaica to Panama (figures 17–18) again shows the same slope as the more eastern North-South profile made in 1933; but in our next profile from 1934 (figures 19–20) topographic complications serve to obscure to some extent the general slope of the water layers although it still remains distinct, but with a rise at the extreme northeastern end where a counter current occurs.

The 1933 profile from Honduras via Jamaica to Haiti (figures 21–22) is still more sharply sub-divided topographically. Southwest of Jamaica the maximum salinity layer appears to be almost free from general slope, while the isohalines both above and below show a slope in the normal direction. Between Jamaica and Haiti on the other hand the slope has been completely reversed except in the closest proximity of Jamaica.

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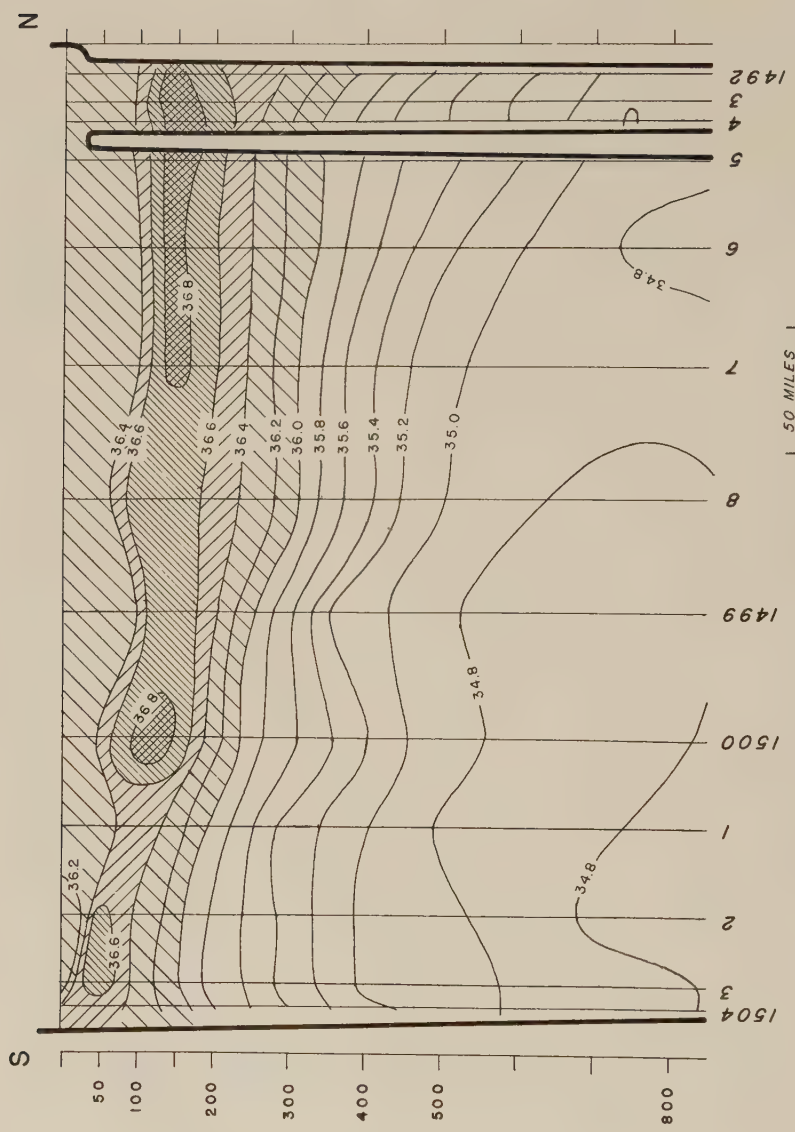

Fig. 5. Salinity profile from Virgin Islands to the north coast of South America.

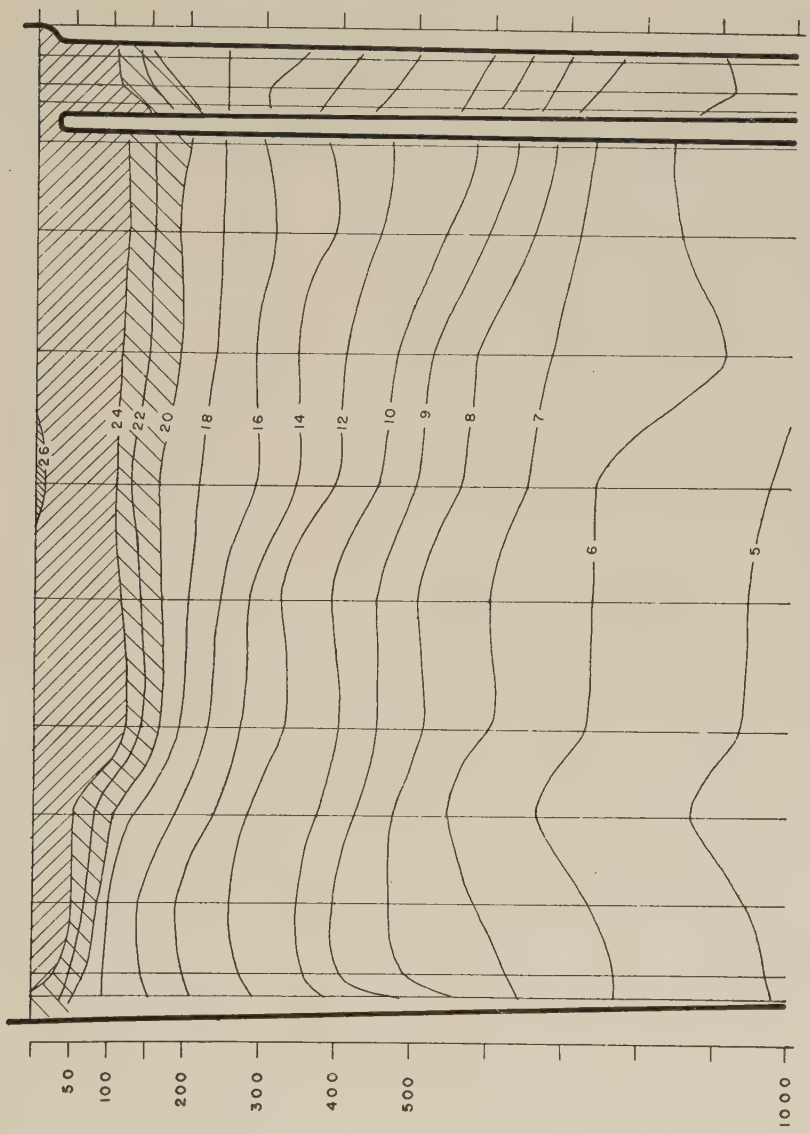

Fig. 6. Temperature profile from Virgin Islands to the north coast of South America.

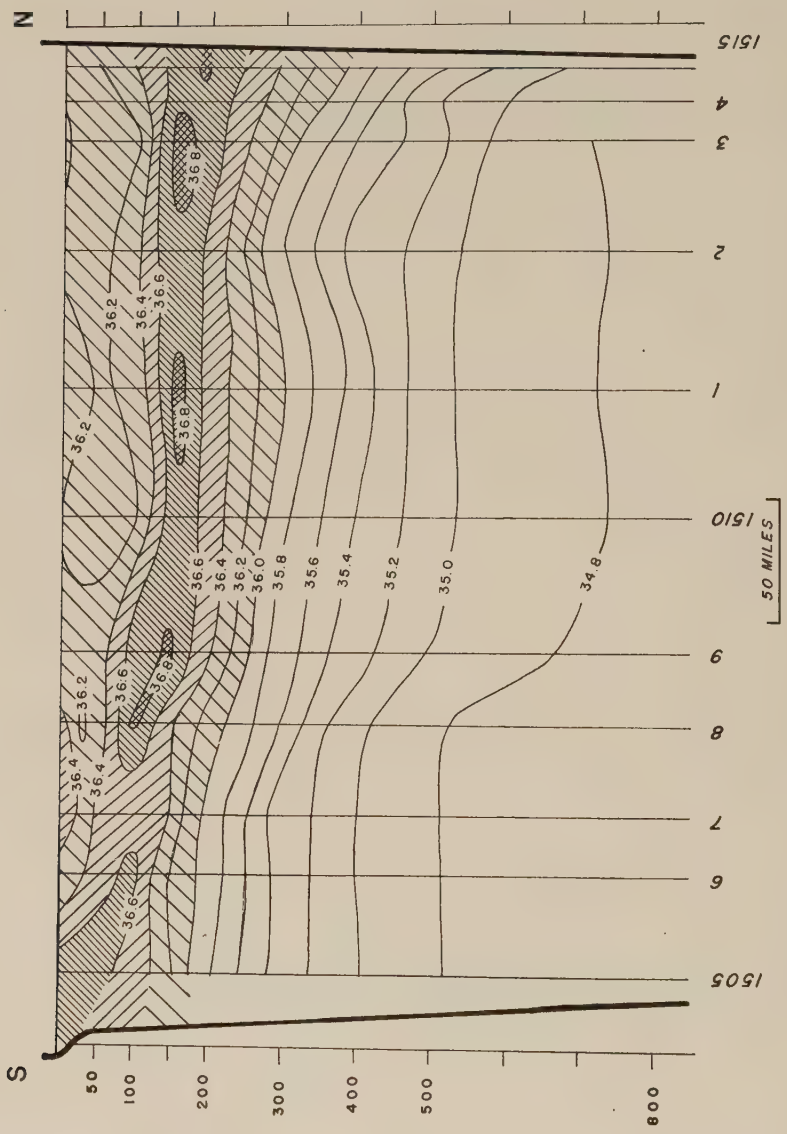

Fig. 7. Salinity profile from the eastern end of Haiti to the north coast of South America.

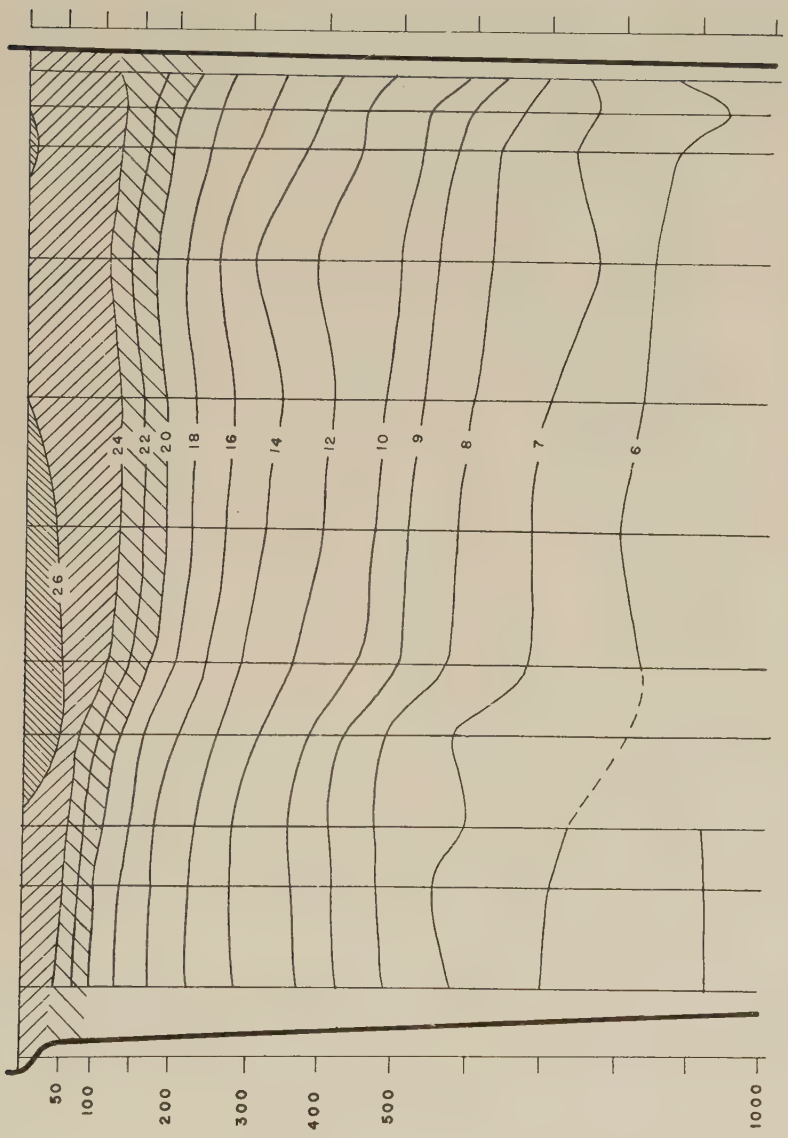

Fig. 8. Temperature profile from the eastern end of Haiti to the north coast of South America.

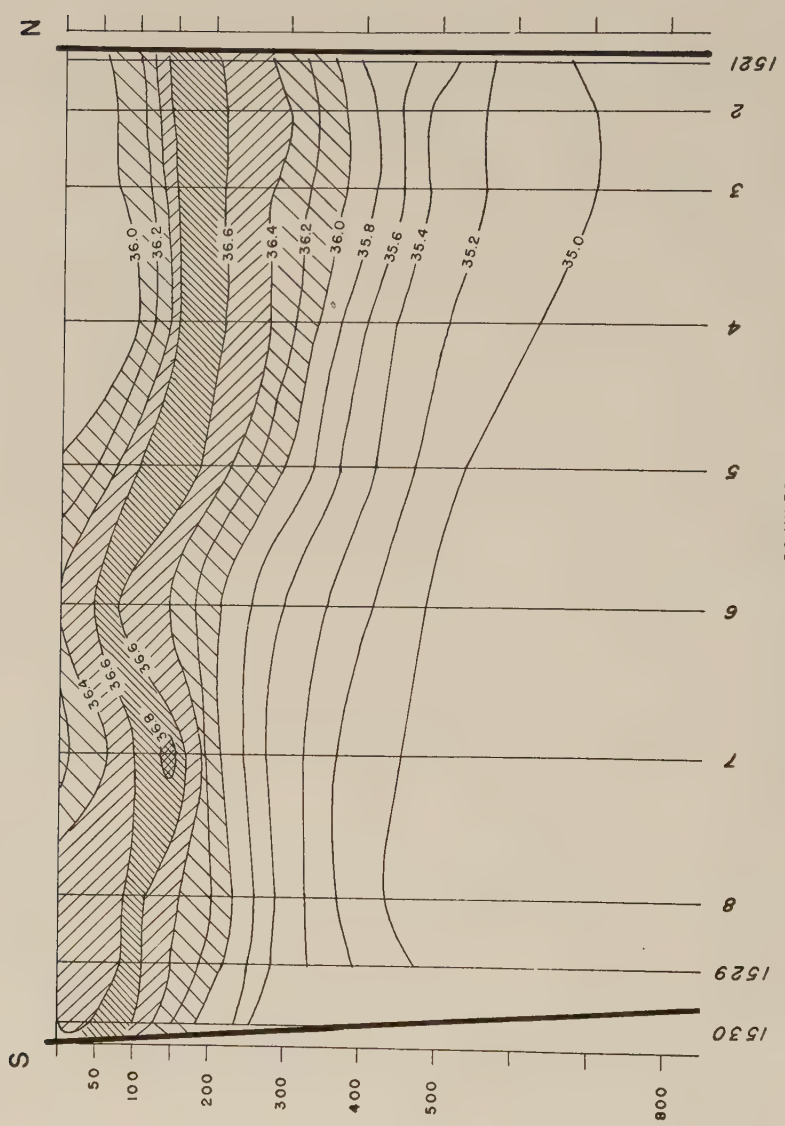

Fig. 9. Salinity profile from western point of Haiti to Colombia.

Fig. 10. Temperature profile from western point of Haiti to Colombia.

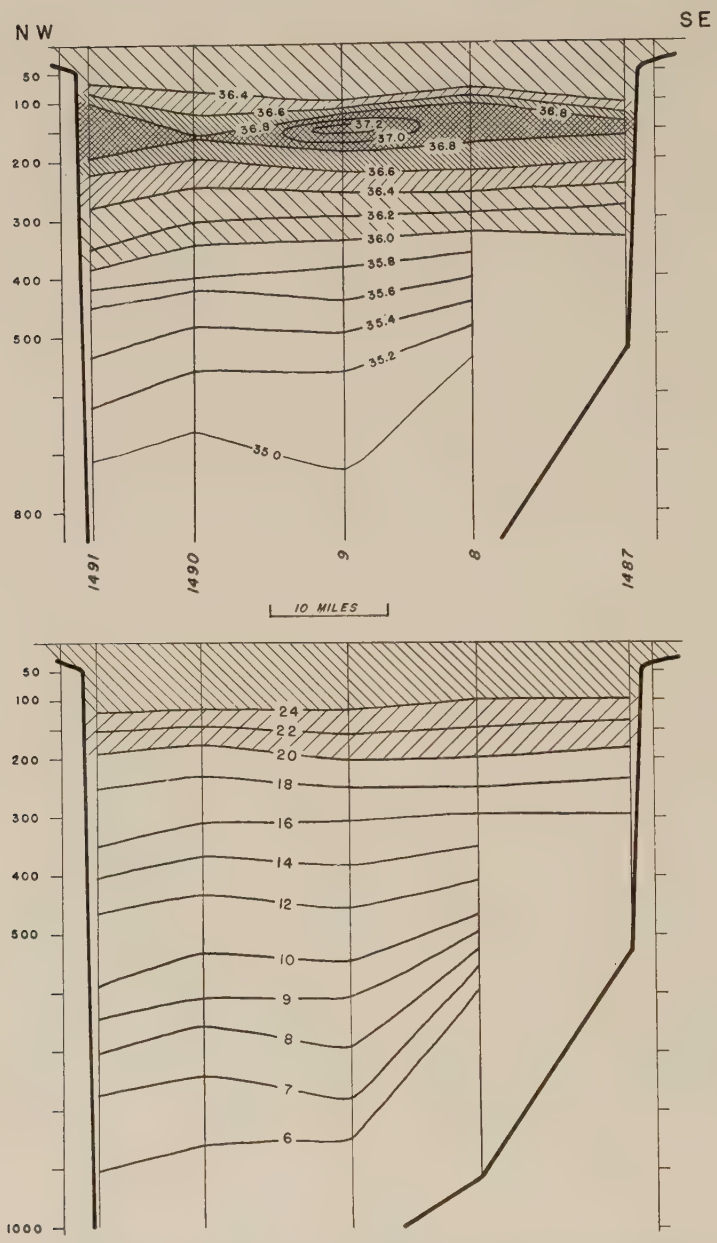

Fig. 11. Salinity profile (*above*) and temperature profile (*below*) of Anegada passage.

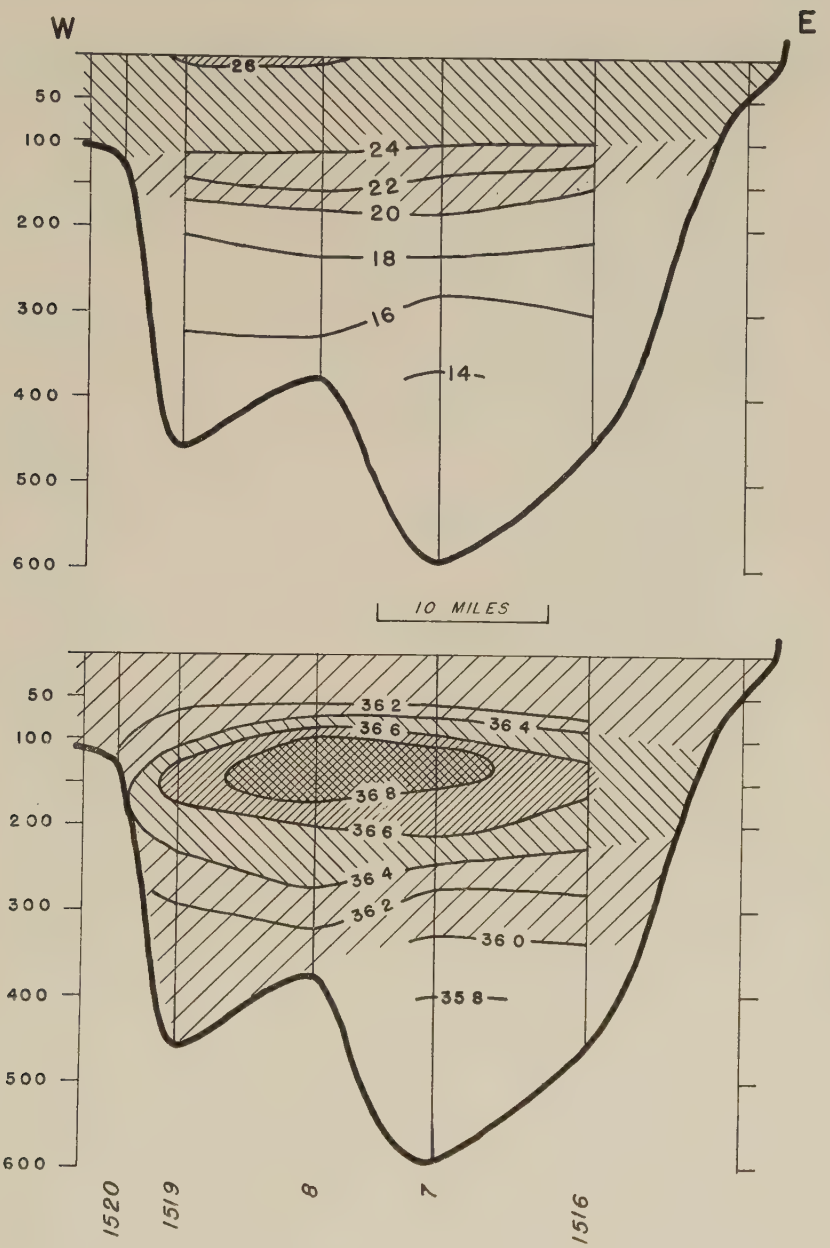

Fig. 12. Temperature profile (*above*) and salinity profile (*below*) of Mona Passage.

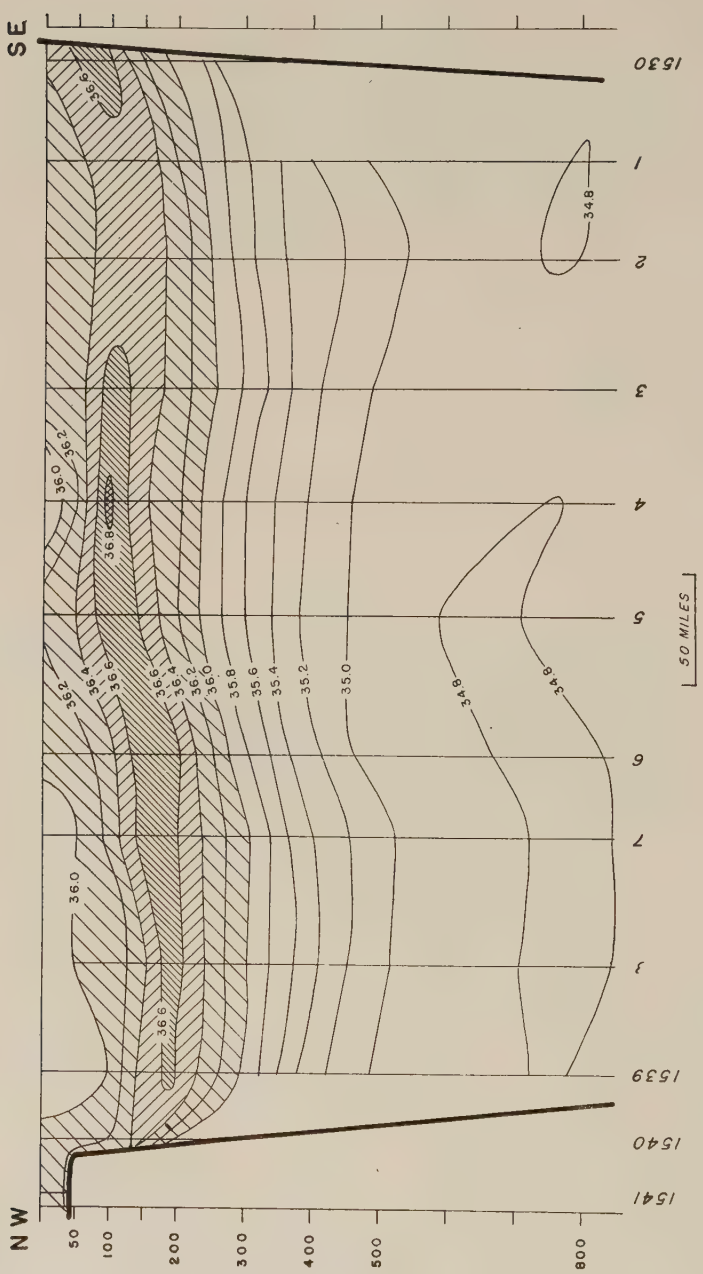

Fig. 13. Salinity profile Northwest-Southeast from Honduras to Colombia.

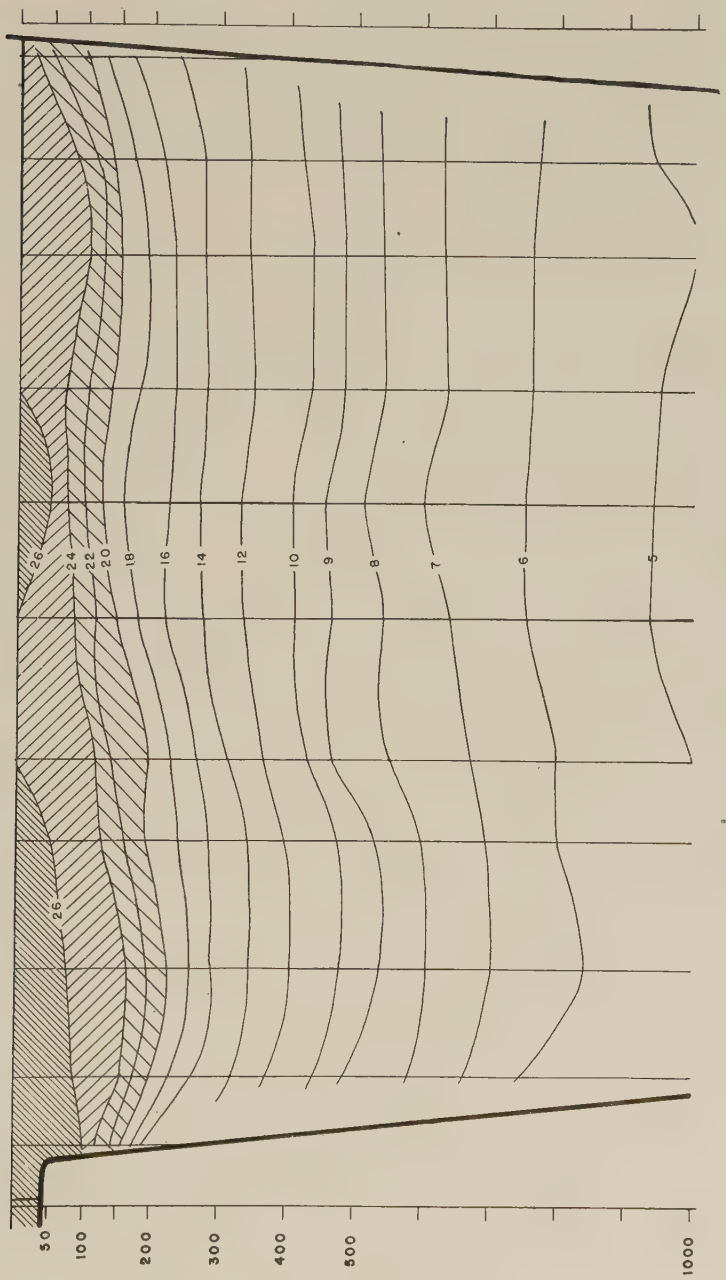

Fig. 14. Temperature profile Northwest-Southeast from Honduras to Colombia.

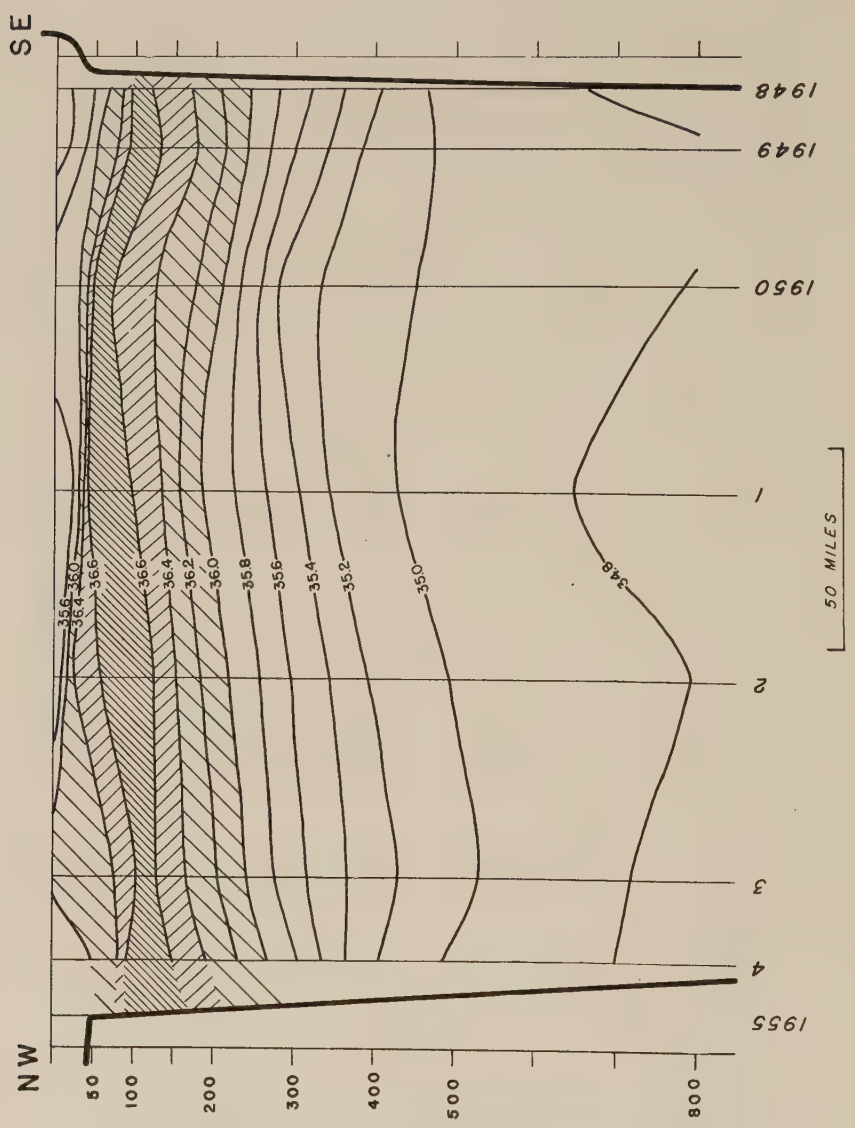

Fig. 15. Southeast-Northwest salinity profile from Panama to Costa Rica.

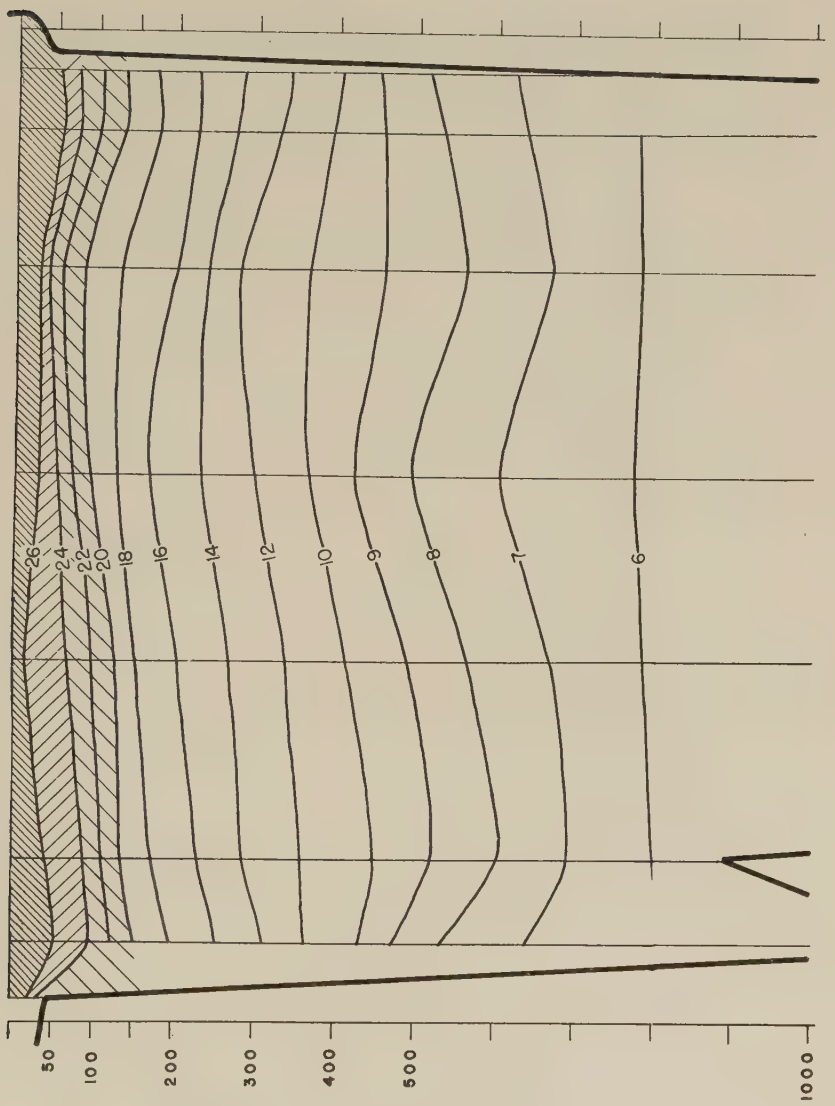

Fig. 16. Southeast-Northwest temperature profile from Panama to Costa Rica.

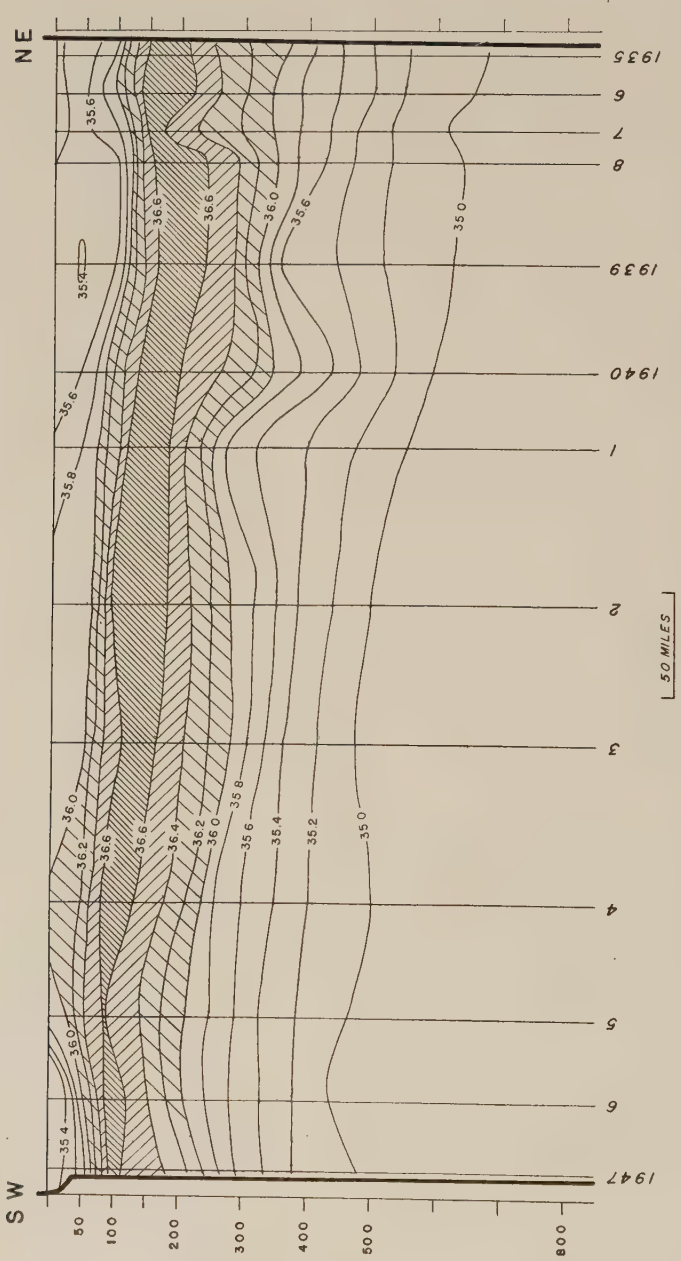

Fig. 17. Northeast-Southwest salinity profile from Jamaica to Panama.

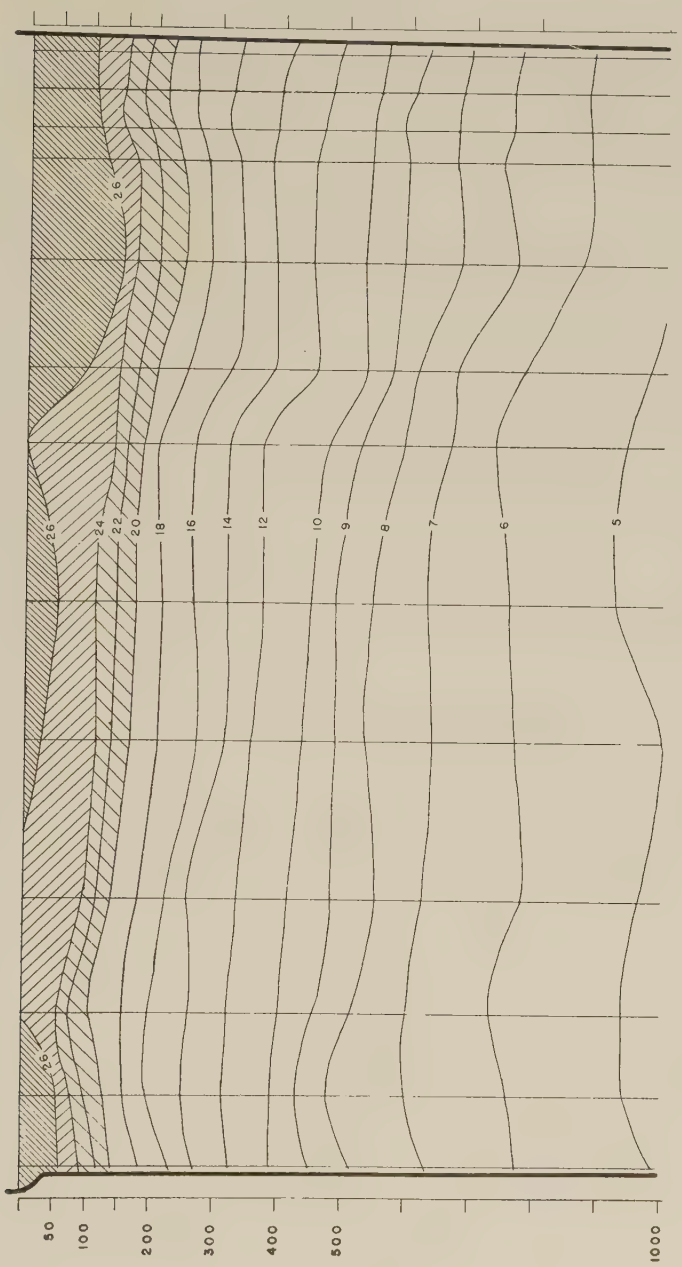

Fig. 18. Northeast-Southwest temperature profile from Jamaica to Panama.

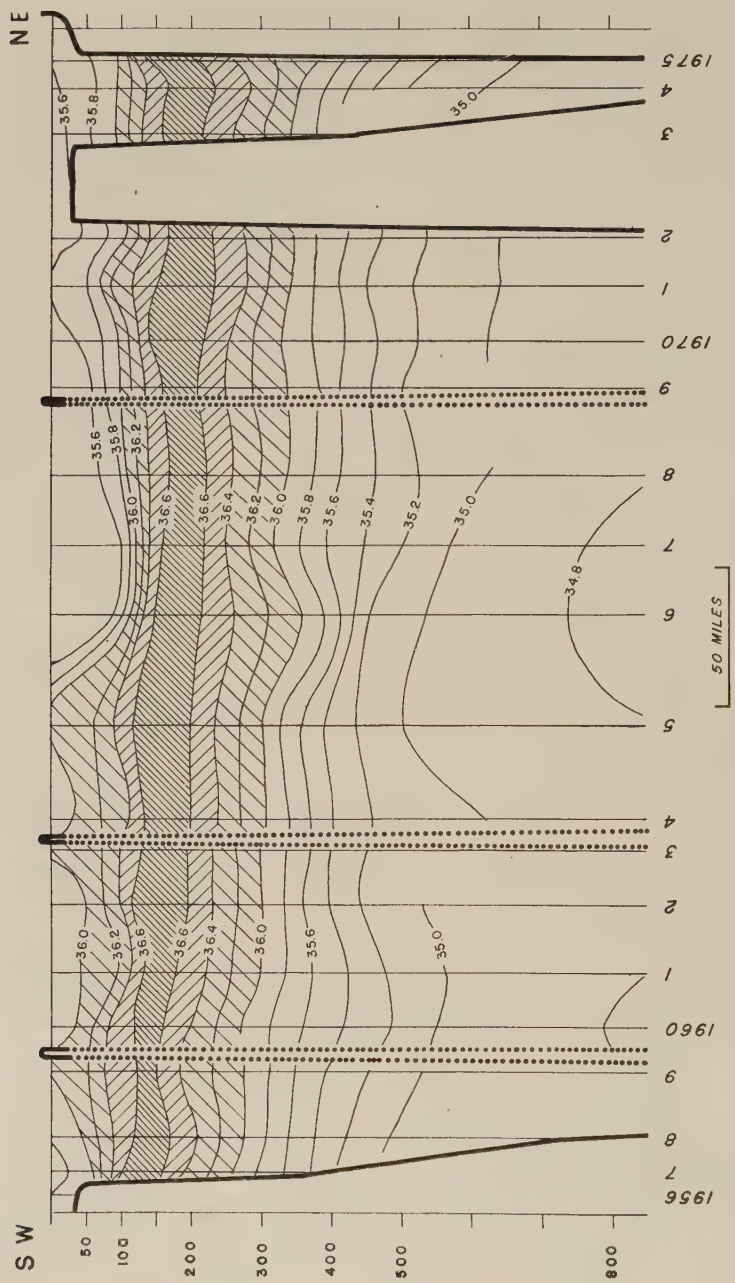

Fig. 19. Southwest-Northeast salinity profile, Nicaragua, old Providence, RoncadorBank, Bajo Nuevo, Pedro Bank, Jamaica.

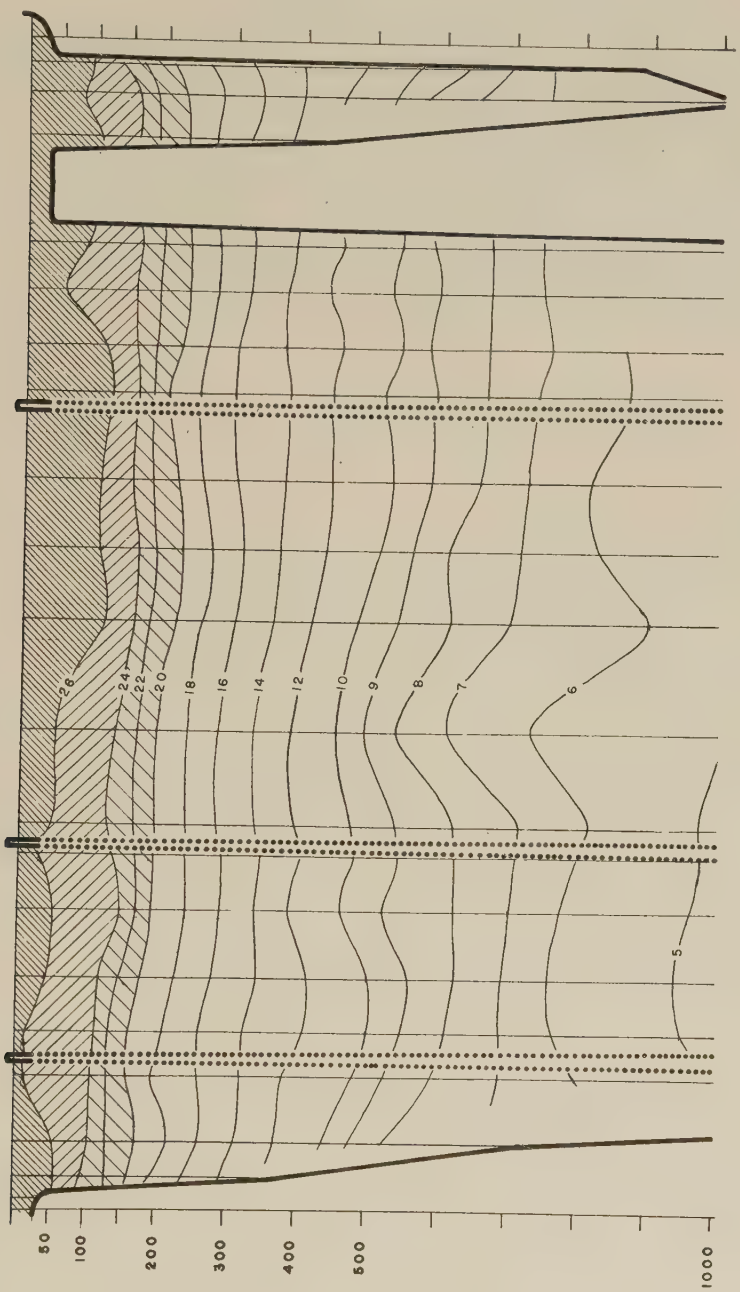

Fig. 20. Southwest-Northeast temperature profile, Nicaragua, old Providence, Roncador Bank, Bajo Nuevo, Pedro Bank, Jamaica.

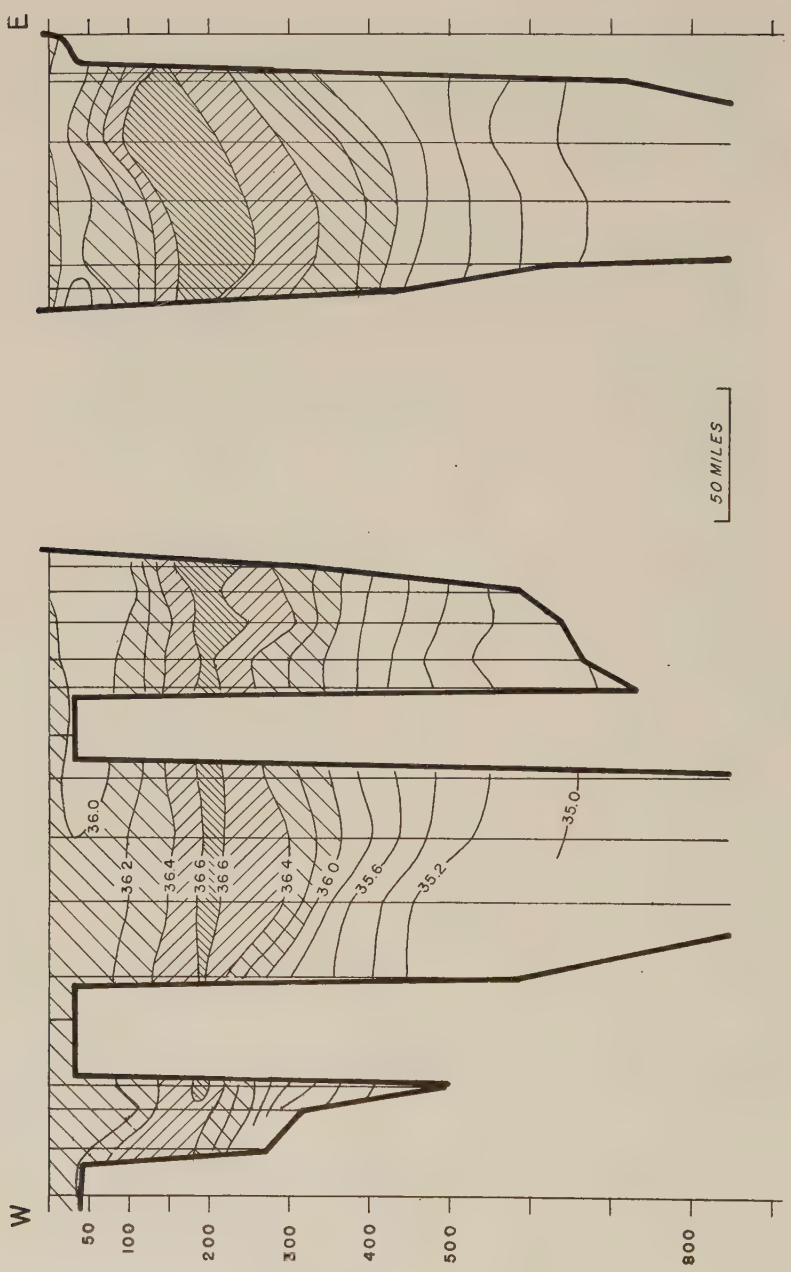

Fig. 21. Salinity profile, Honduras-Jamaica-Haiti.

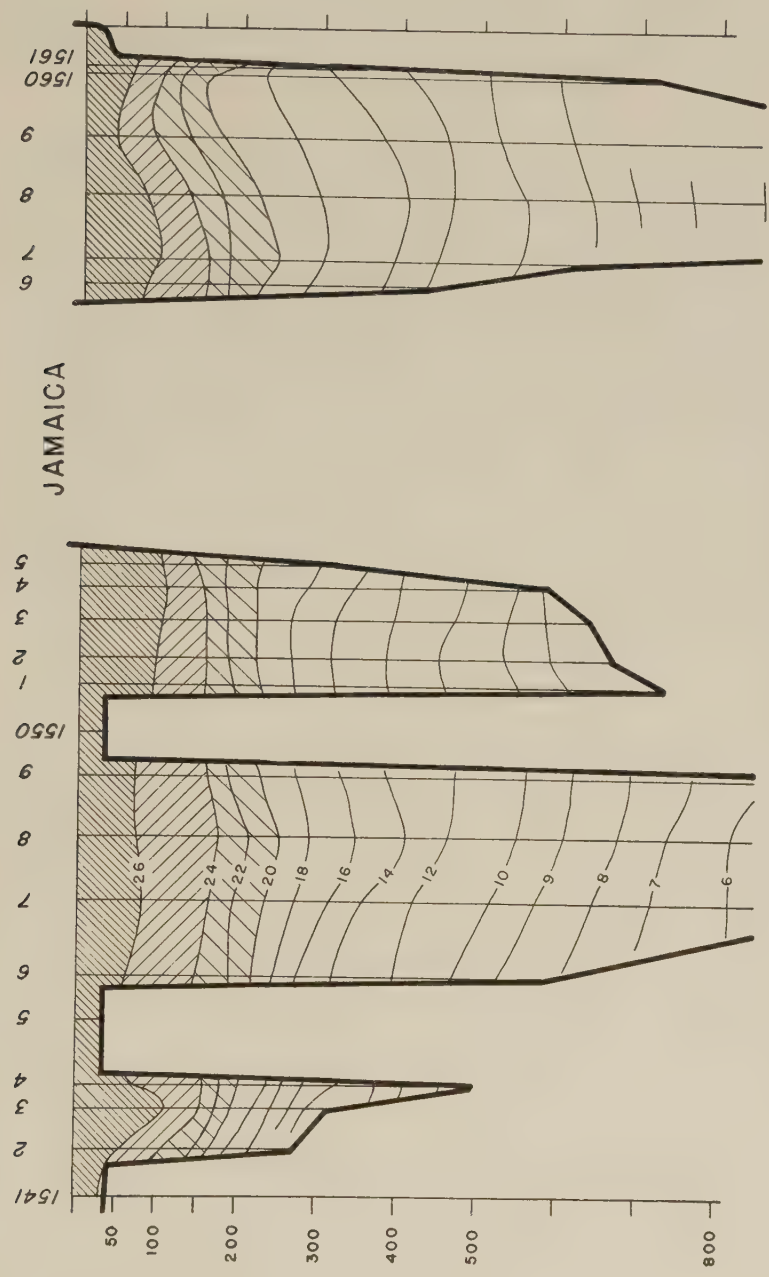

Fig. 22. Temperature profile, Honduras-Jamaica-Haiti.

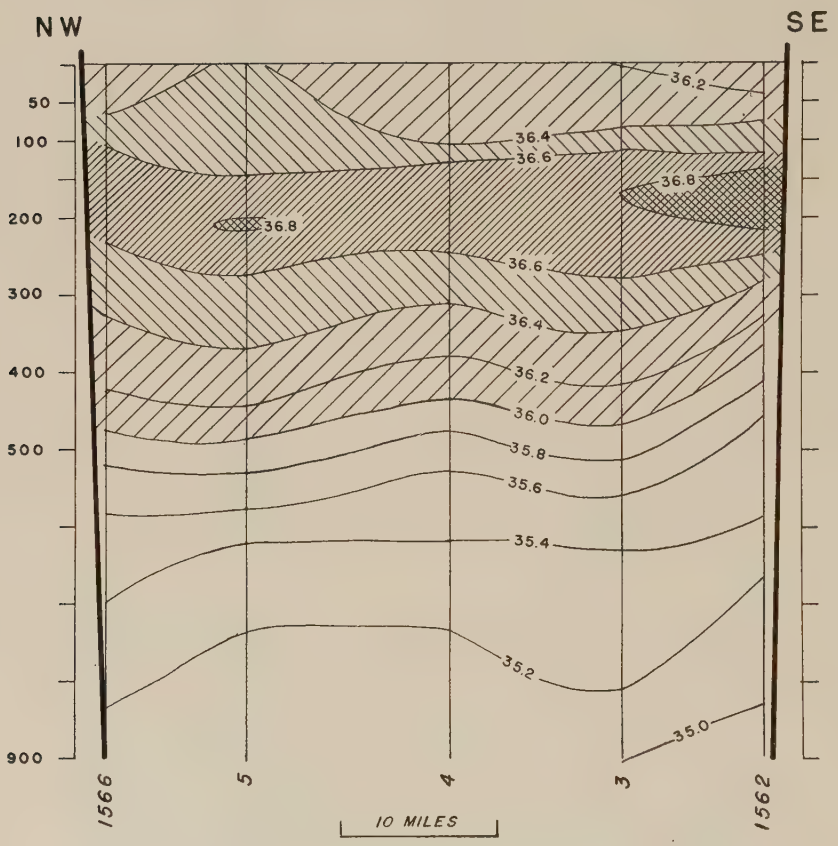

Fig. 23. Salinity profile. Windward Passage.

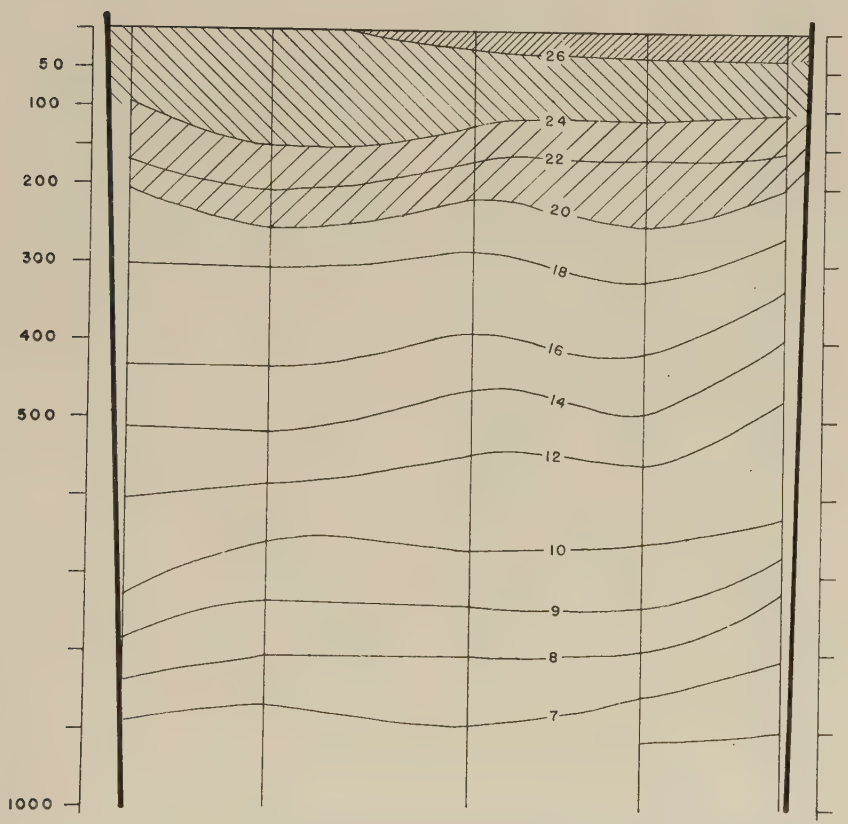

Fig. 24. Temperature profile. Windward Passage.

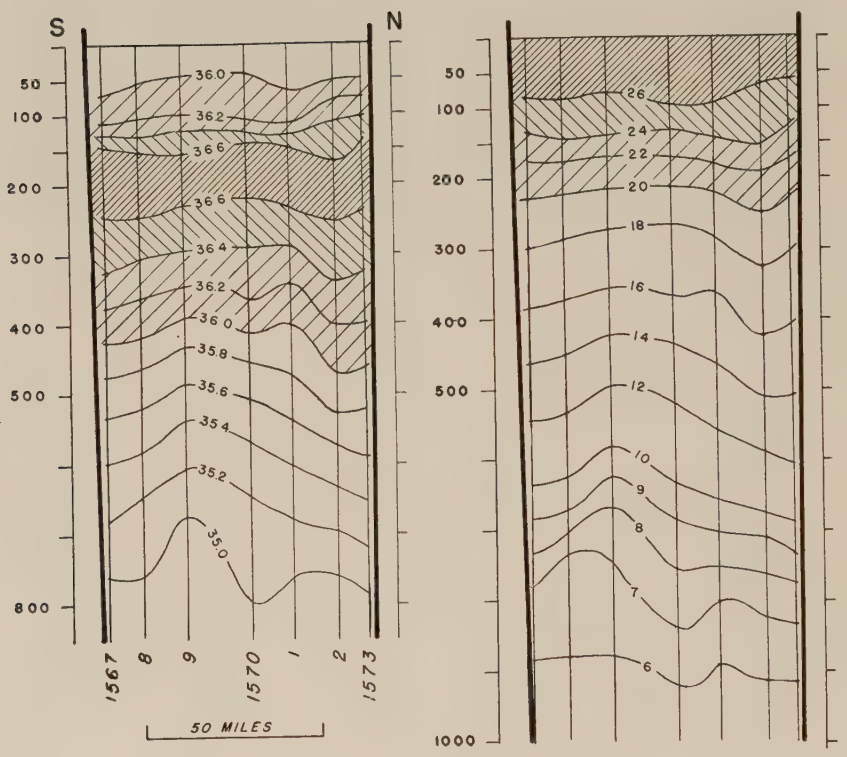

Fig. 25. Salinity profile (*left*) and temperature profile (*right*) between Cuba and Jamaica.

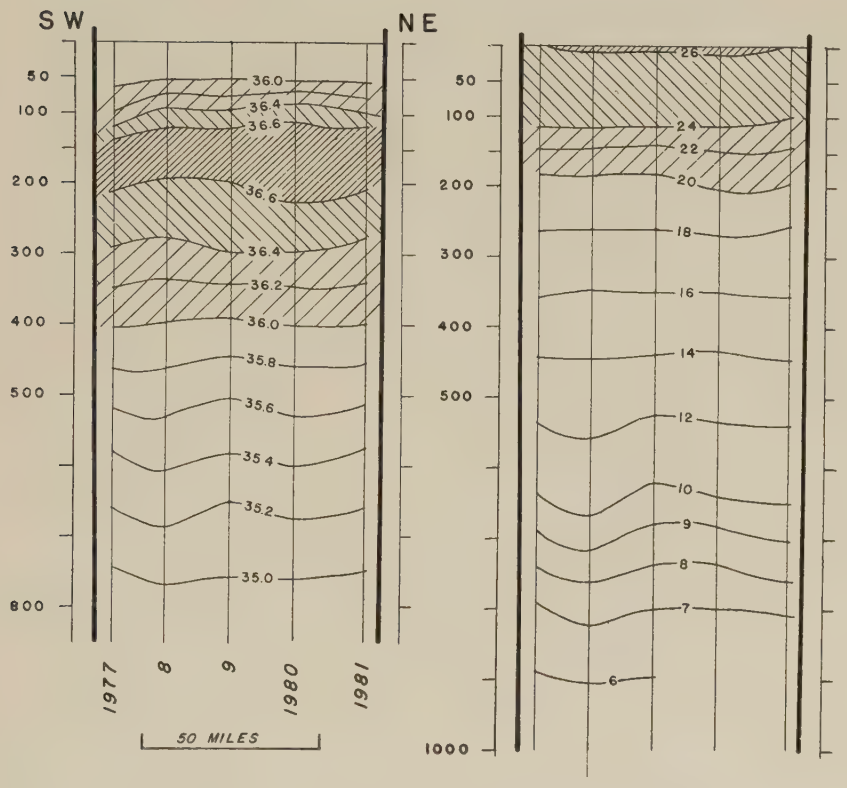

Fig. 26. Salinity profile (*left*) and temperature profile (*right*) from Cayman Brac to Cuba.

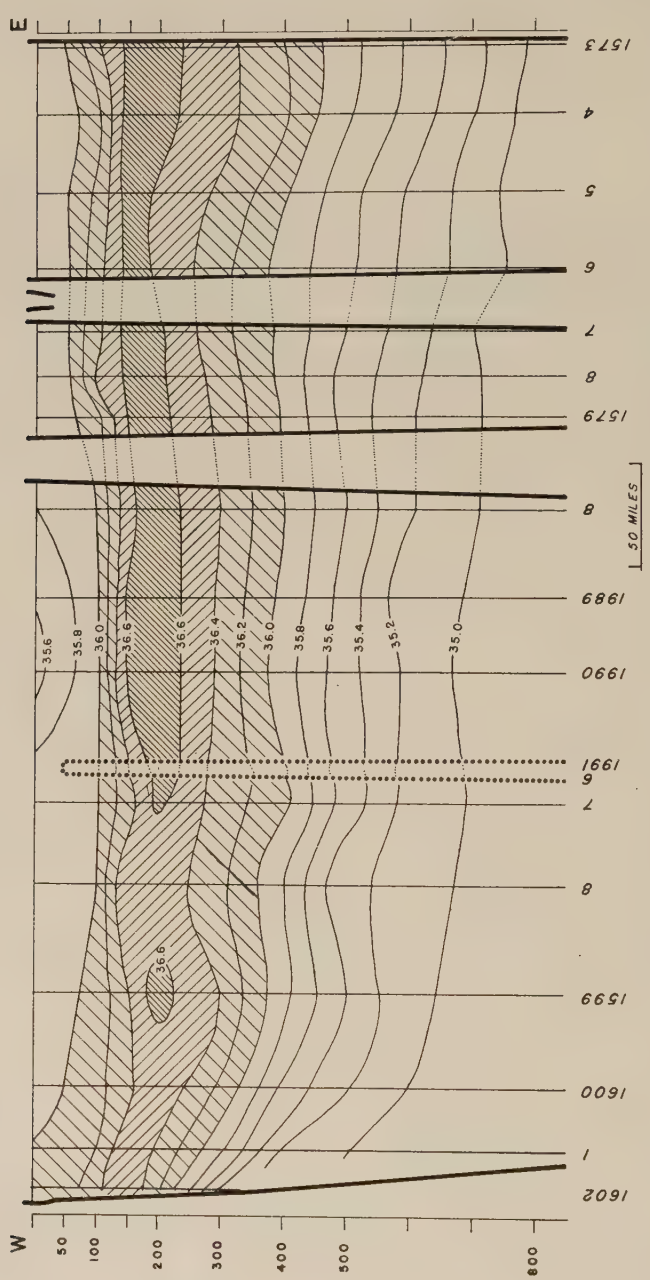

Fig. 27. Salinity profile. Cuba-Cayman Brac-Grand Cayman-Misteriosa Bank-British Honduras. Combination of 1933 and 1934 observations.

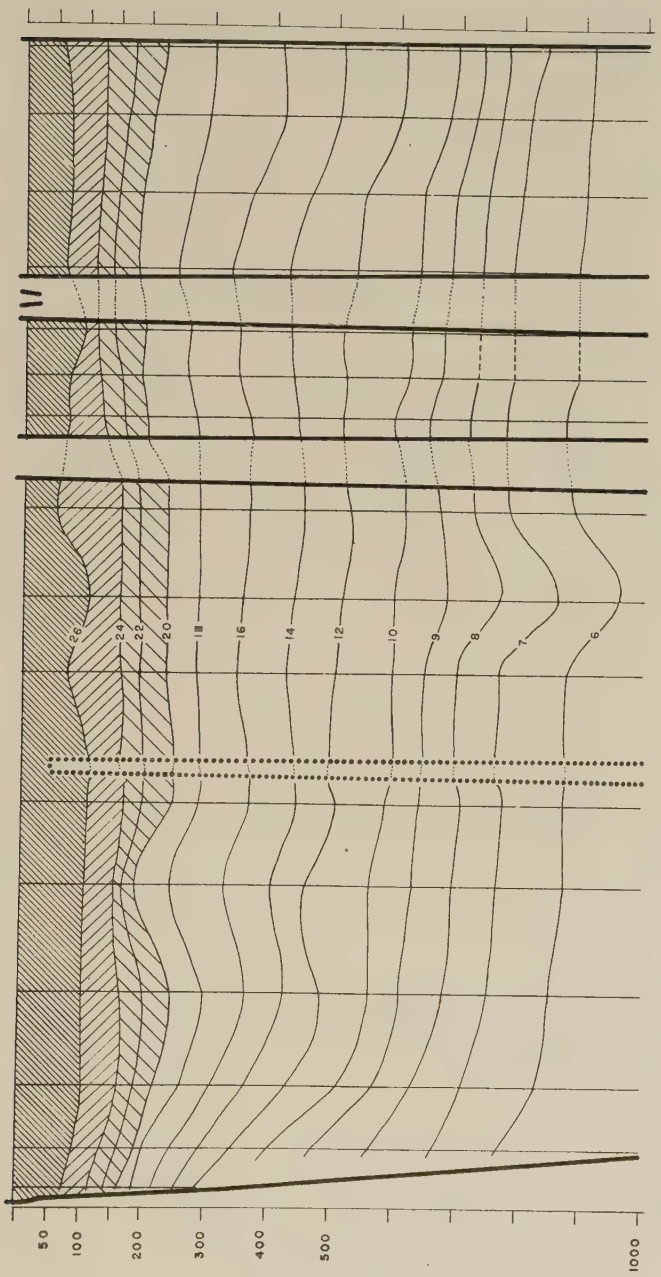

Fig. 28. Temperature profile. Cuba-Cayman Brac-Grand Cayman-Misteriosa Bank-British Honduras. Combination of 1933 and 1934 observations.

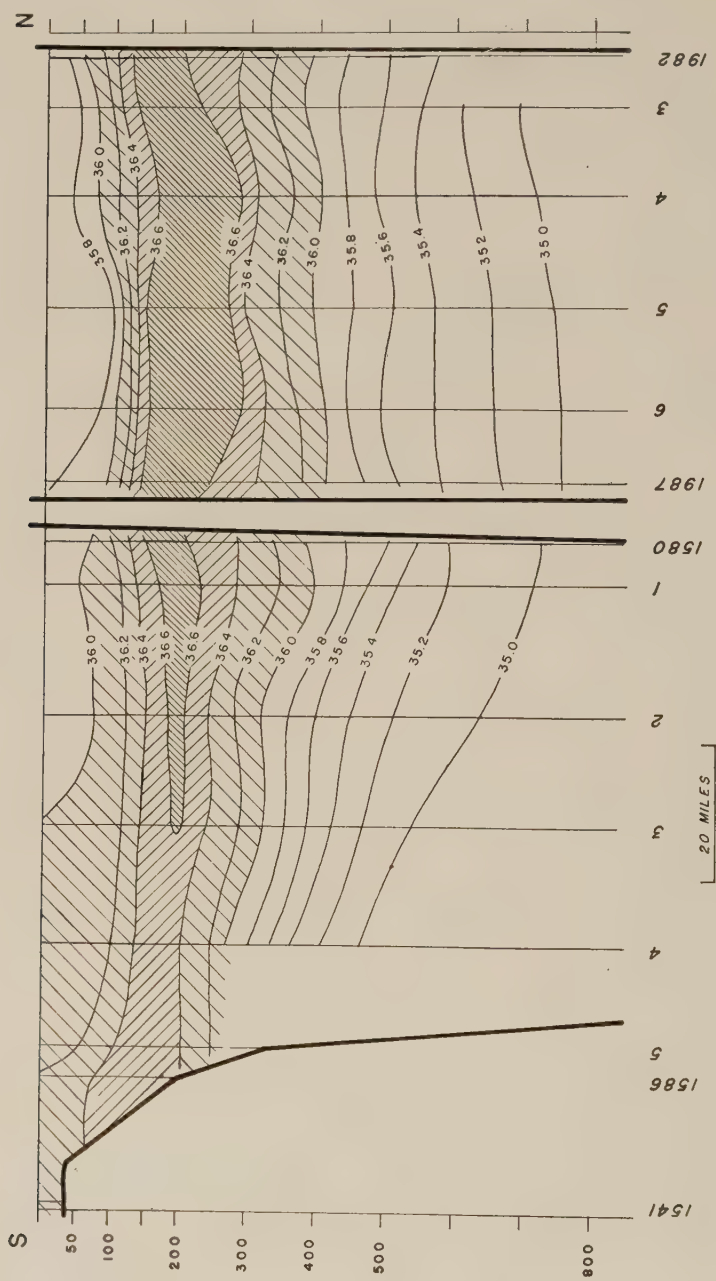

Fig. 29. Salinity profile. Cuba-Grand Cayman-Mosquito Bank. Combination of 1933 and 1934 observations.

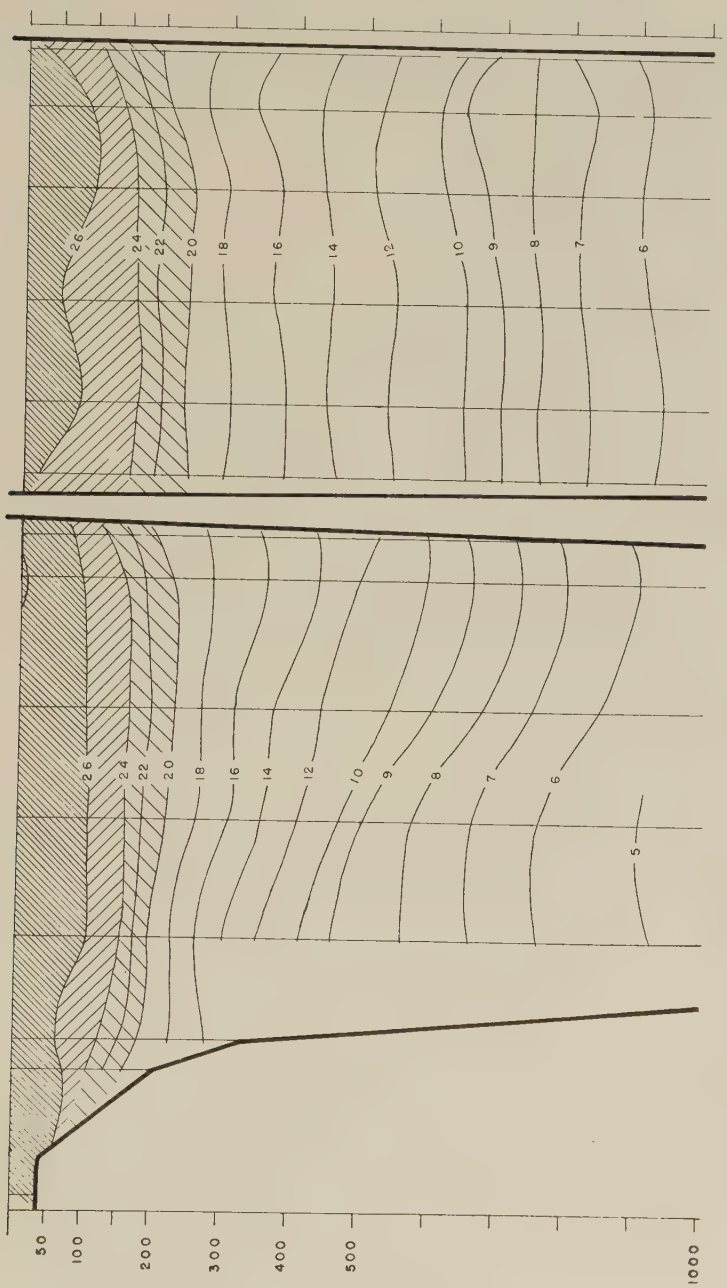

Fig. 30. Temperature profile. Cuba-Grand Cayman-Mosquito Bank. Combination of 1933 and 1934 observations.

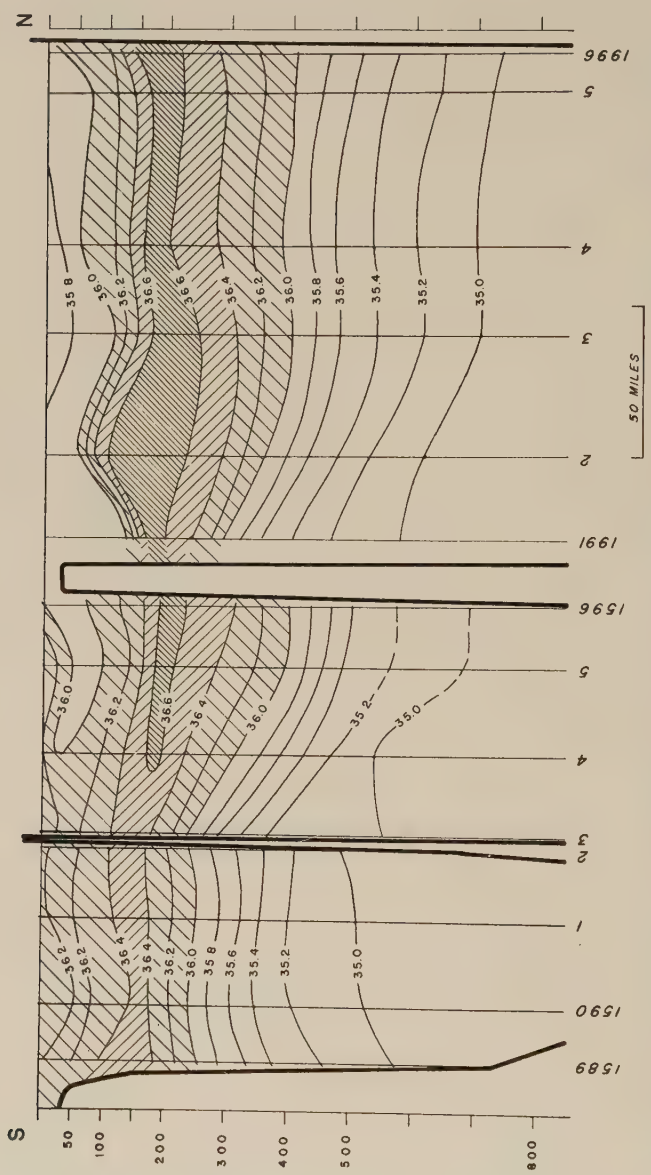

Fig. 31. Salinity profile. Cuba-Misteriosa Bank-Swan Island-Honduras. Combination of 1933 and 1934 observations.

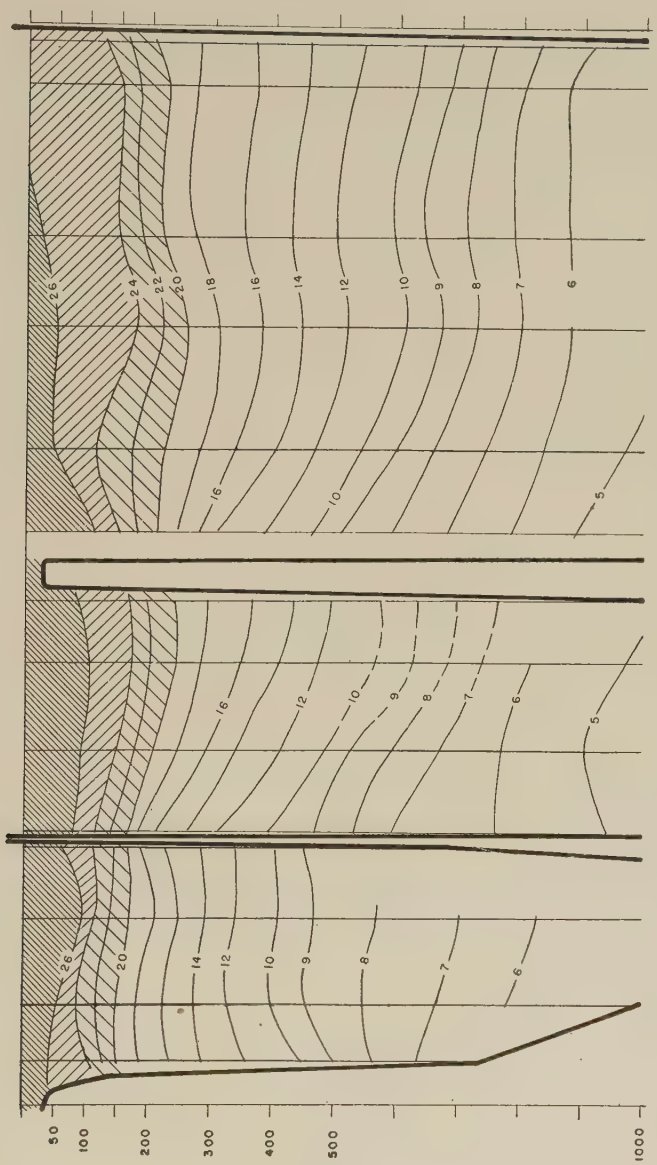

Fig. 32. Temperature profile. Cuba-Misteriosa Bank-Swan Island-Honduras. Combination of 1933 and 1934 observations.

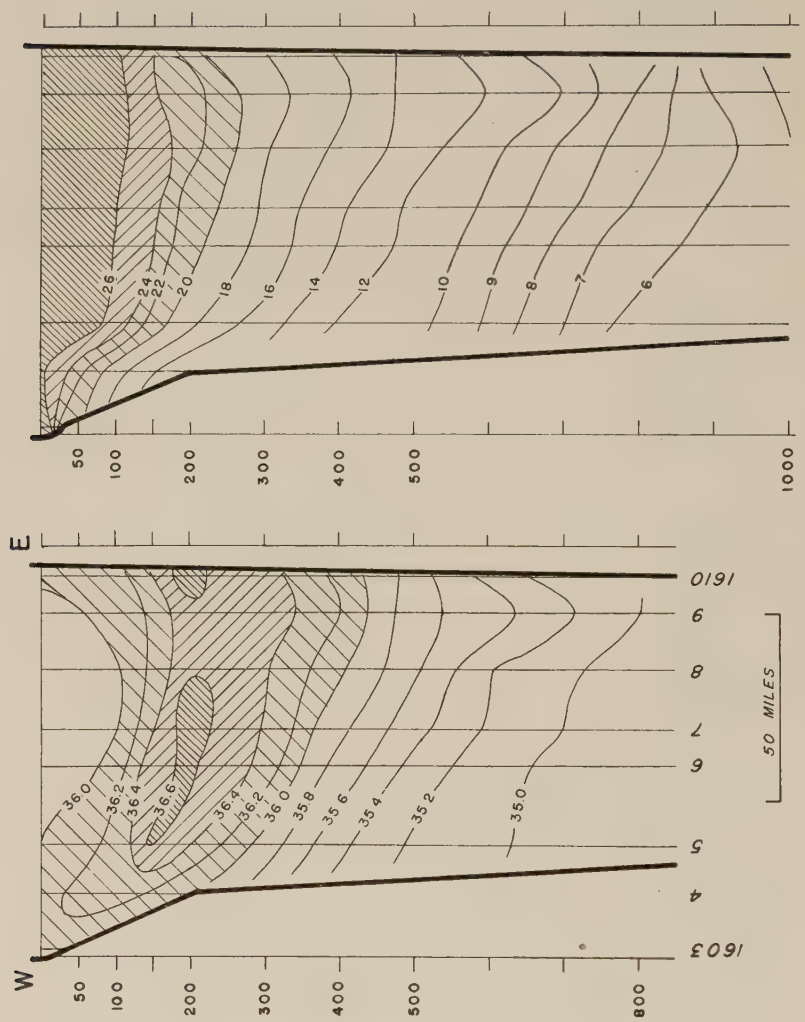

Fig. 33. Salinity profile (*left*) temperature profile (*right*) of Yucatan Channel. 1933.

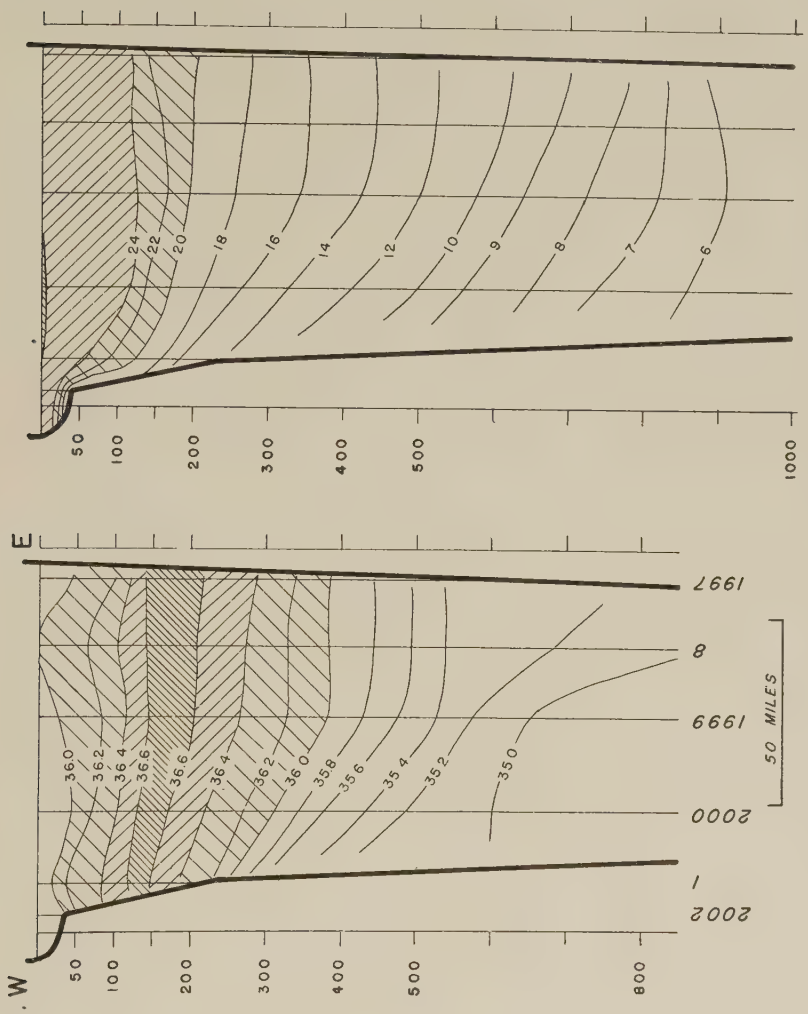

Fig. 34. Salinity profile (*left*) temperature profile (*right*) of Yucatan Channel. 1934.

In the Windward Passage (figures 23–24) the slope is again slight except on the southeastern side where a conspicuous rise occurs.

The profile from Jamaica to Cuba (figure 25) is also comparatively level, although irregular.

Figure 26 is a short Southwest-Northeast profile from Cayman Brac to Cuba with a conspicuous general slope.

Figures 27 and 28 present a longitudinal profile through the Cayman Sea from Cuba to British Honduras and is a composite picture of 1933 and 1934 observations as indicated by the station numbers (St. 1573–79, and 1596–1602 from 1933; St. 1988–91 from 1934). In this case the combination of observations from the two separate years offered no difficulties in spite of the sub-division of the profile by Cayman Brac, Grand Cayman, and Misteriosa Bank. The profile shows a long relatively flat middle section with greater slopes of normal direction at both ends.

Figures 29 and 30 again present a combination of 1933 (St. 1541 and 1580–86) and 1934 (St. 1982–87) observations in which a slight discrepancy without great significance appears to be developed around Grand Cayman Island which divides this profile into two separate sections (observed in separate years).

In figures 31 and 32 greater difficulties were encountered by the combination of 1933 (St. 1589–96) and 1934 (St. 1991–96) observations; the records for 1934 show generally higher levels of all isohalines north of Misteriosa Bank, which separates the 1934 section from the 1933 series, than those found in the southern part in 1933. The discrepancy can only be presented as a fact of observation, since the material does not provide a basis for a discussion of its explanation. It will be noted that the discrepancy was not obtained with regard to temperatures.

Our final profiles (figures 33 and 34) present 1933 and 1934 observations in the Yucatan Channel. It will be noticed that the 1933 observations, which were more complete, show less high salinity water present and a greater slope than indicated in the 1934 observations. The significance of this will appear in a separate report on dynamics.

Horizontal Variations in Vertical Distributions

Due to the slope of the Caribbean water masses already before mentioned considerable horizontal differences in vertical distribution

are found to occur in the Central American seas. The nature of this effect is exemplified by the bathymetric topography of the isothermal surface of 15° C. shown in figure 35. In this figure one will first notice a general transverse slope, particularly well shown in the Caribbean where it extends from less than 200 meters depth in the Southeast to more than 350 meters in the North. We furthermore observe a longitudinal increase in the depth of the entire isothermal surface particularly on its deepest side as we pass from the Caribbean into the Cayman Sea, where 15° C. occurs below 400 meters north of the Grand Cayman and also between Cuba and Jamaica. The combination of 1933 and 1934 observation, which has also given difficulties on other points, produces certain irregularities in the bathymetric distribution of 15° C. in the bight between Honduras, Colombia and Panama, which may illustrate a normal situation or may merely present a composite picture of two different sets of conditions.

Another important feature of the horizontal variations in vertical distributions is found in the variations in the thickness of the maximum salinity layer, reckoned by salinities higher than $36.6^0/_{00}$ as shown in figure 36. This picture has some general features in common with the bathymetric topography of 15° C. in that the thickness increases from complete absence (0) in the South, and in general on the left side of the main flow, to more than a hundred meters in the North within the Caribbean proper; and that it also shows a longitudinal increase from the northern Caribbean to the Cayman Sea, where it exceeds 125 meters thickness north of Grand Cayman. It is important to notice however that the gradient of thickness is not uniform as is the gradient of the 15° C. isothermal surface, but on the contrary shows localized but consistent variations, which, when compared with figure 53 (p. 74), show a definite relationship to the current system of the Central American seas.

The comparatively thick streak in the southern part of the eastern Caribbean follows exactly the line of the probable main current to the region south of Jamaica where it ends in a large eddy located in that vicinity; while the thick portion in the north and northeast is associated with relatively stationary waters along the northern margin of the Caribbean. The thickened portion in the middle of the bight between Honduras, Colombia and Panama also occupies a comparatively stationary region between the main current and the southwestern eddy (see p. 73), and the very thick portion in the

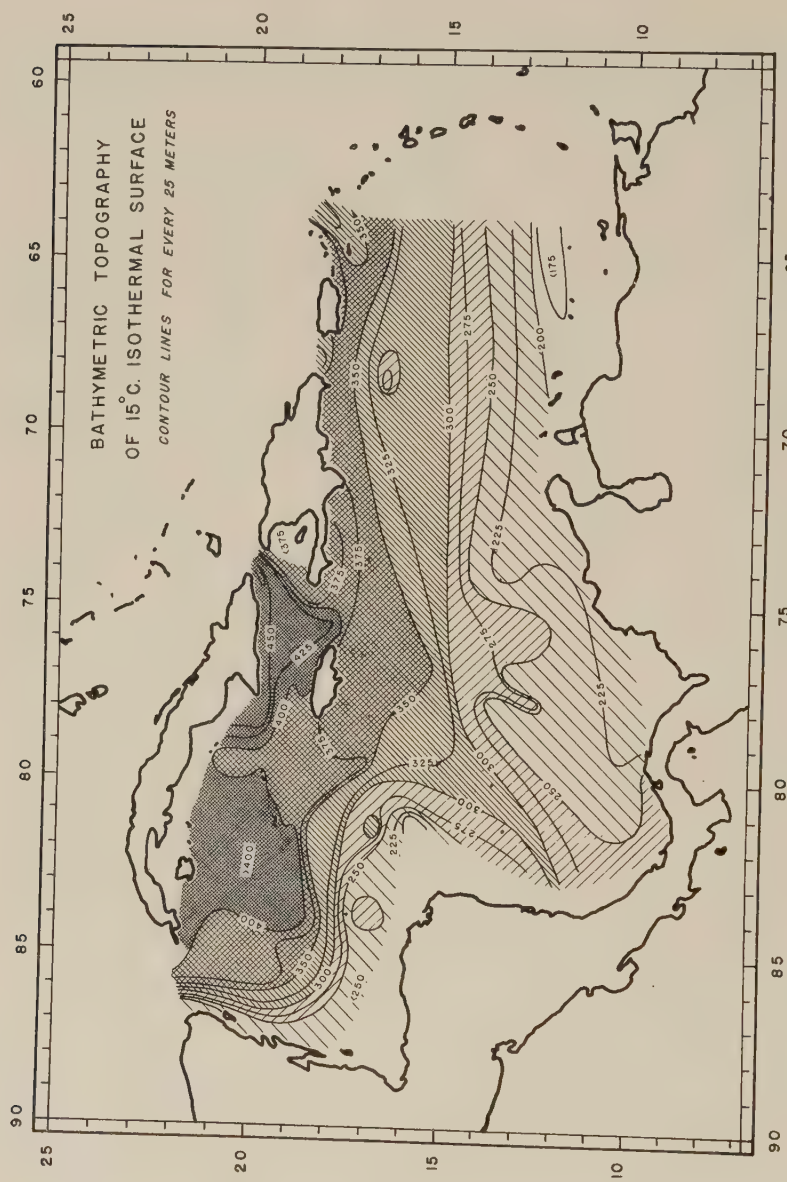

Fig. 35. Bathymetric topography of the 15° C. isothermal surface.

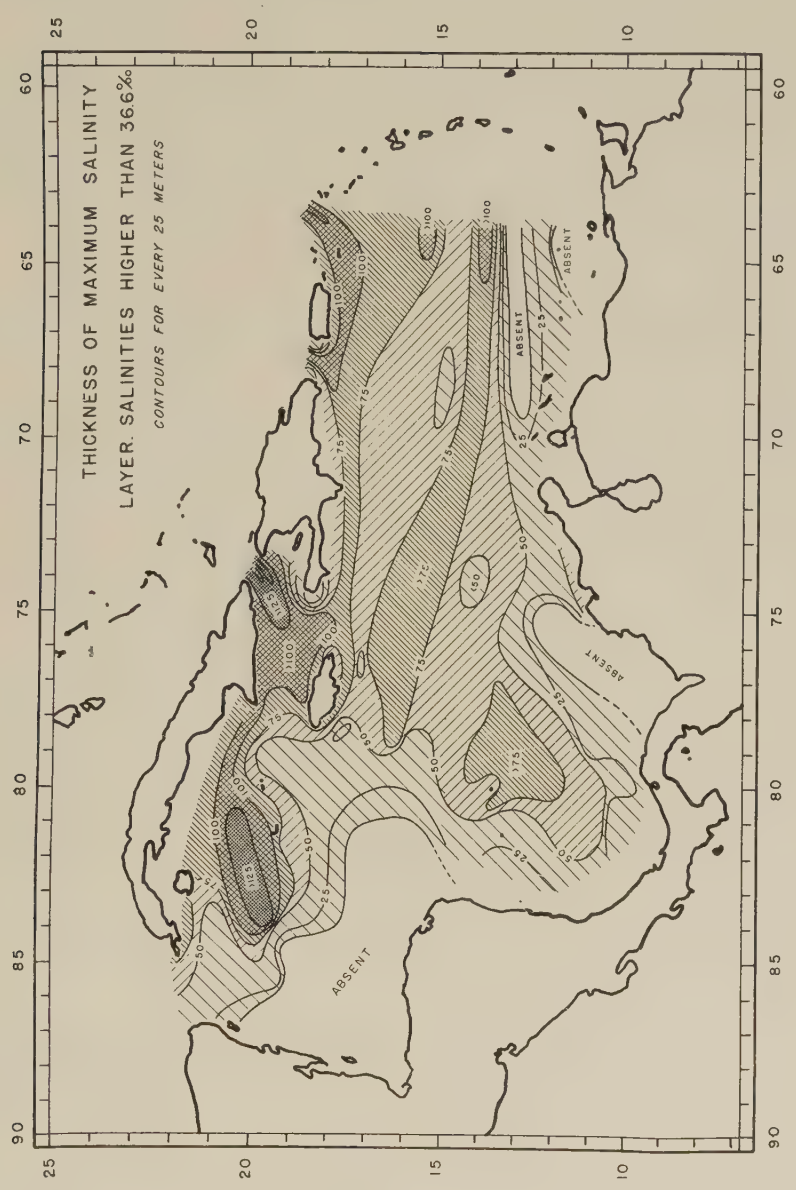

Fig. 36. Thickness of maximum salinity layer (salinities higher than 36.6 ‰).

northern Cayman Sea is associated with the counter currents and eddy system of that region.

That local variations associated with the general circulation pattern are more pronounced in the thickness of the maximum salinity layer than in the bathymetric topography of the 15° C. isothermal sheet is obviously due to the higher level and greater current speeds of the former.

Adiabatic Temperature Changes

The bottom waters of the Central American seas in general, and in some of the deeper troughs in particular, furnish excellent illustrations of the effect of adiabatic heating, as shown in figure 37; but it is important for the question of origins and circulation (see below) to notice that when we correct for the adiabatic effect a slight gradient of decreasing temperatures remains all the way down to deepest bottom. For reasons to be discussed later, adiabatic temperature curves have been drawn for the observed average temperatures at 2000 and at 2500 decibars, and the *potential temperature curve for average temperatures in situ at all levels* reduced to one atmosphere's pressure is also presented. From the level of minimum temperatures in situ, at about 2000 decibars, down to 6000 decibars, the curve of potential temperatures at the surface calculated from average observations at all levels shows a decrease of about 0.12° C. Approximately the same value is obtained when we subtract the adiabatic temperature curve for observed average temperature at 2000 decibars from the curve of actual average temperatures in situ at all levels below; while a similar subtraction from 2500 decibars down to 6000 gives a decrease of about 0.065° C.[1] While slight, these gradients are of significant magnitude with reference to the accuracy of observations, showing originally colder water to be present at the deeper levels all the way down.

Threshold Depths and Bottom Water

Figure 38 shows the vertical temperature and salinity curve for one station in the Anegada Passage (St. 1491), one immediately inside the Caribbean between St. Thomas and St. Croix, Virgin Islands, (St. 1493) and two from the straits between Cuba and Jamaica (St.

[1] The curves drawn in broken line or dot and dash at the right in each fragment of Fig. 37 show the average temperatures which ought to prevail below 2000, respectively 2500 meters depth if adiabatic temperature increases had not been offset by actual differences in potential temperatures.

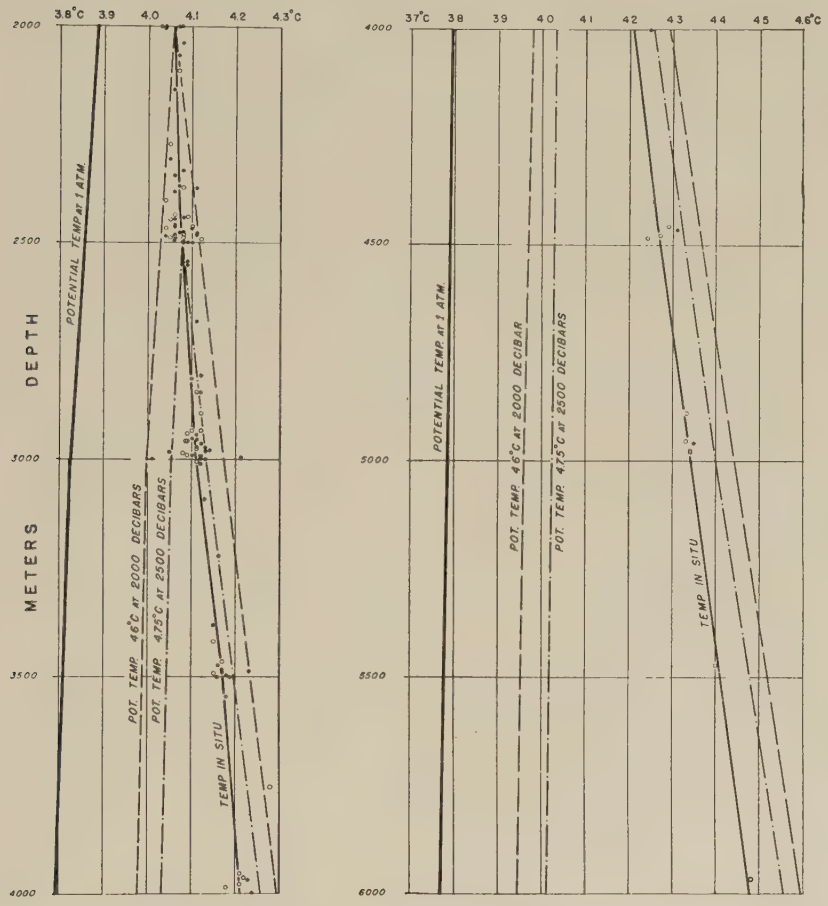

Fig. 37. Scatter diagram of all temperature observations below 2000 meters depth in the Caribbean and Cayman seas with calculated adiabatic curves, and a fair curve of average temperatures *in situ*. See text.

1569 and 1570). The first two curves were selected because they represent the only two instances in which temperatures in situ below 4° C. were observed inside of the Caribbean in the course of the entire survey. Their location near one of the main inlets from the open Atlantic is therefore significant (see p. 76). The other two curves (St. 1569–70) are, on the other hand, entirely typical of the bottom waters of all the Central American ocean basins (except with reference to the depth of minimum temperature, see below).

From this figure it will be seen that the salinities in all four cases reach a constant value for all deeper levels at about 1500–1800 meters depth, that is, beyond this depth they only fluctuate between $34.96^0/_{00}$ and $34.99^0/_{00}$, a fluctuation within $\pm$ $0.015^0/_{00}$ which is within the practical error of the salinity determinations. The average salinity of the Caribbean bottom waters computed from 204 determinations below the isotherm of 4.10° C. is $34.979^0/_{00}$.

Since a thick layer of constant salinity around approximately this value, extending from the isotherm of about 4° C. downward, is present also in the Anegada Passage itself, and has likewise been observed in other regions of the Western Atlantic (Iselin 1936) it is evident that the depth of constant salinity cannot in this instance be taken to indicate the depth of the lowest effective threshold level. For a determination of the latter we must therefore return to a study of the depths of minimum temperatures.

The minimum temperatures in situ shown in figure 38 represent the inflection points on the curves between decreasing temperatures above, due to different origins, and increasing temperatures below, due to adiabatic heating. For precise determination of lowest effective threshold level[1] one should actually consider potential temperatures only since the threshold must occur at the *outside* level of the minimum potential temperature observed inside. For practical purposes however, a determination of the depth of minimum temperature in situ inside will generally suffice to indicate the actually effective threshhold level in first approximation. A computation from 136 tempera-

[1] By lowest effective threshhold level we refer to the lowest level at which an exchange of waters in significant quantities actually does occur, which need by no means always be identical with the lowest topographic threshhold, although it would probably be found to be the same in the case of Caribbean due to the hydrographic relationship between the Central American seas and the open Atlantic (see p. 75).

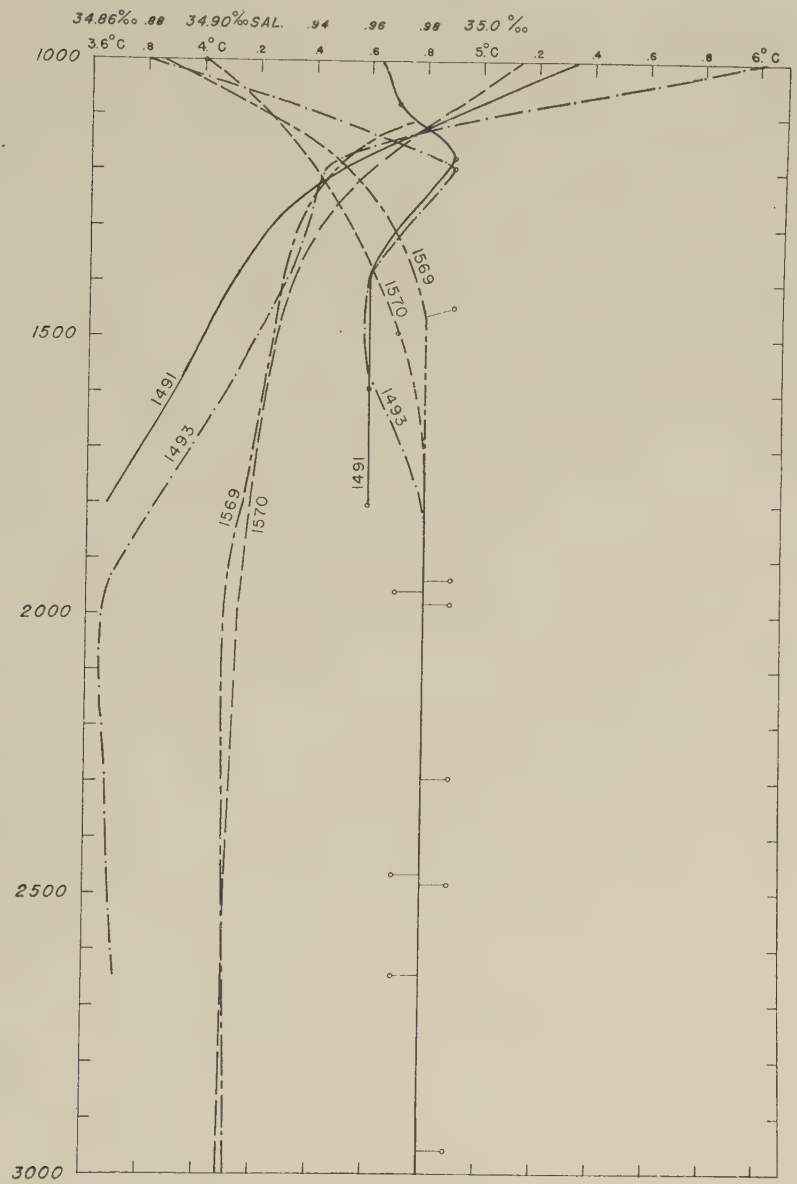

Fig. 38. Temperature and salinity curves below 1000 meters. Selected stations. See text.

ture observations in the Central American seas between 4.10° C. and minimum temperatures in situ gives an average of 4.069° C.

A study of the horizontal distribution of the depths of minimum temperatures in situ reveals an interesting and significant difference between the Caribbean proper, South and East of the ridge connecting Haiti, Jamaica and Honduras, and the Cayman Sea between this ridge and the Yucatan Channel. In the Caribbean proper the average depth of minimum temperature, determined from 27 series from 1933 extending below the temperature inflection point, is 2088 meters, with a total range of 1836–2495 (?) meters; 9 series from 1934 giving 2013 meters with a range of 1922–2193. For the Caiman Sea, North of the Jamaican Ridge, 13 series from 1933 gave an average depth of minimum temperature of 2533 meters, with a total range of 2373–2986. Only 3 of the 1934 series from the Caiman Sea extend deep enough for a determination of minimum temperature, and these are located off to one side between Caiman Brac and Cuba but it is notable that two of these three series are the only two from that year with minimum temperatures occurring below 2200 meters depth.

It thus seems indicated that the bottom waters of the Caiman Sea must enter over a somewhat lower threshhold (about 2500 meters depth), which can only be found in the Windward Passage, than the lowest effective threshhold (about 2000–2100 meters) over which the bottom waters enter the Caribbean proper. This conclusion directly implies that the bottom waters of the Caribbean proper and of the Caiman Sea although virtually undifferentiable by their standard physical and chemical characteristics (temperature and salinity) must actually be entirely distinct bodies of separate external origins and must remain separate within the Central American basin at least below about 2000–2100 meters depth.

HORIZONTAL DISTRIBUTIONS

In our presentation of distributions in horizontal perspective we shall confine ourselves to a consideration of salinities only. Since the surface temperatures are generally very uniform within the Caribbean region, and a considerable proportion of the slight variations observed were undoubtedly due to the progression of seasonal heating during the time it took to complete the part of the survey undertaken in each of the two early spring seasons of 1933 and 1934,

a plot of the observed surface temperatures gives a rather meaningless picture, not worth presenting. The really significant regional differences in surface temperatures will appear from the various vertical profiles discussed in the preceding chapter. It will suffice at this point to call attention to the fact that due to the slope of the water masses there is a general tendency for the surface temperatures to be somewhat lower along the southern and western margins of the Caribbean, than in the north and northeast; the tendency being particularly pronounced in the eastern area where the surface temperature generally drops 1–2° C. from North to South. In the deeper layers the temperatures and salinities are so closely correlated that separate illustrations of the horizontal distributions of each would seem superfluous; particularly when we concern ourselves with the distribution of the central cores of the maximum and minimum salinity layers, which are of virtually identical temperature throughout regardless of their salinity values, as one may see from the temperature-salinity correlation curves (figures 58–82).

Figure 39 shows the distribution of salinities in the surface layer in 1933, based upon observations at 25 meters depth in view of the fact that some suspicion attaches to the determinations for the surface itself made during that year (see page 5). In figure 40 we have for comparison the surface salinities observed in 1934. It will be seen that the surface salinities in the latter year were very much lower than in 1933, nowhere exceeding $36.2^0/_{00}$, even reaching as low as $35.4–35.6^0/_{00}$ south of Jamaica and below $35.4^0/_{00}$ off the Central American coast. In 1933 surface salinities lower than $35.8^0/_{00}$ were not observed, and salinities higher than $36.6^0/_{00}$ occupy a band of considerable width along the north coast of South America.

In spite of these great differences in absolute values, in the two years, there is nevertheless a general agreement in the main features of the *relative* distribution of salinities in each year. In both years relatively high salinities are indicated in the wide Central American bight between Colombia and Honduras. Both years show an area of relatively low salinities south of Jamaica and a similar area off the southwest coast of Cuba. The 1933 observations show the intrusion of higher surface salinities through the Windward Passage, narrowly connecting, between Jamaica and Cuba, with the intermediate salinities ($36.0–36.2^0/_{00}$) surrounding the minimum south of Jamaica. In 1934 these higher salinities were only encountered at one single

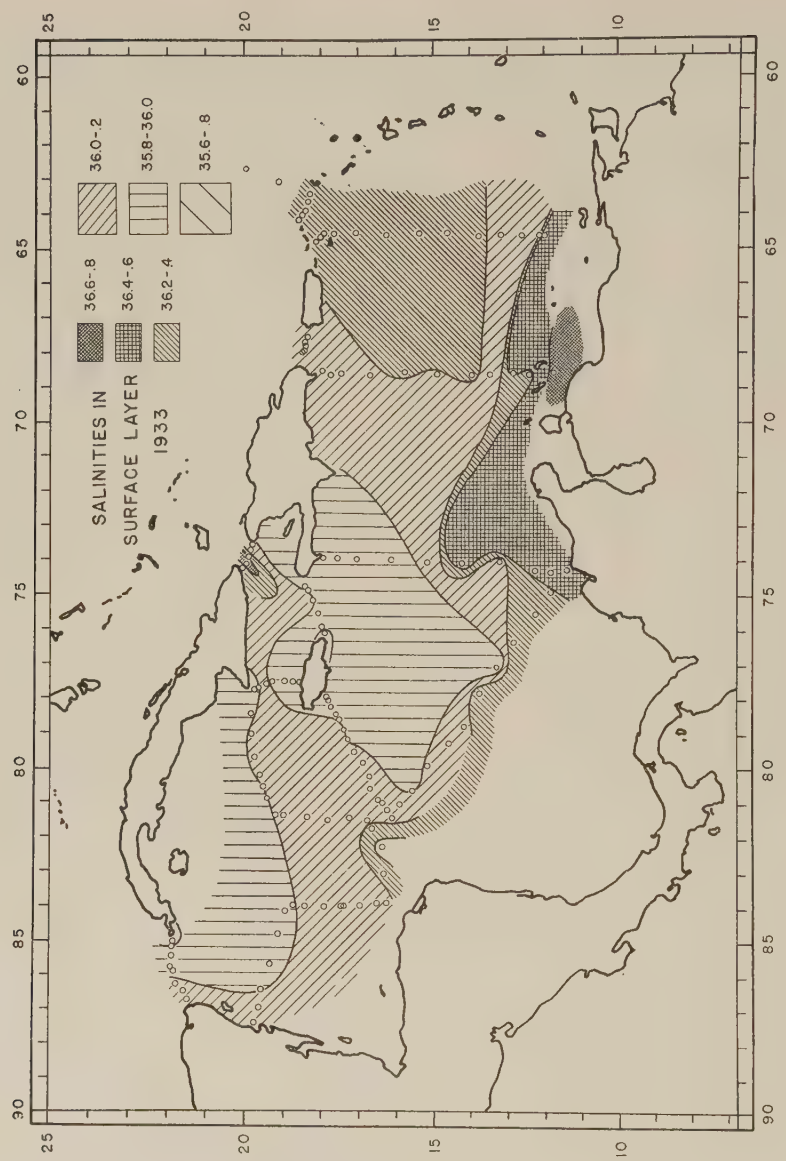

Fig. 39. Distribution of salinities in the surface layers in 1933.

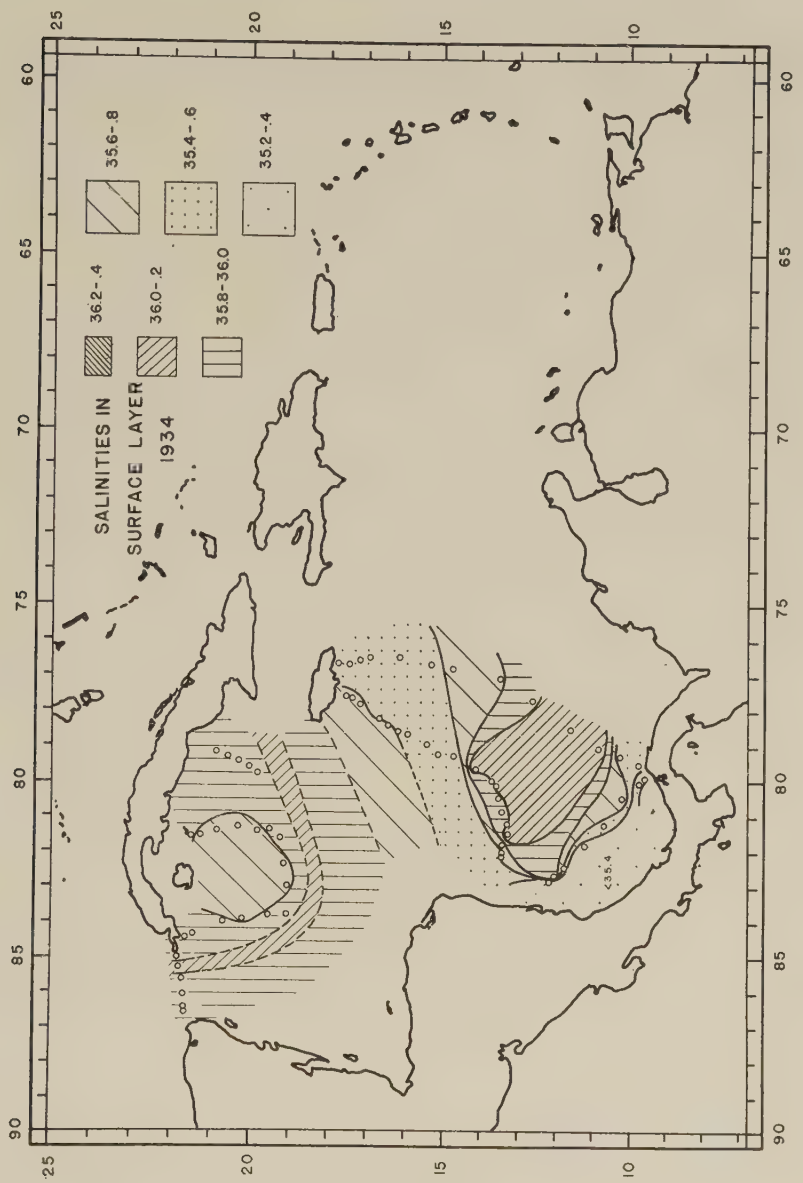

Fig. 40. Distribution of salinities in the surface layers in 1934.

station in the Yucatan Channel; and when a corresponding band (sal. 36.0–36.2‰) has been drawn around the salinity minimum south of Cuba towards the passage between Cuba and Jamaica, this is merely a matter of very tenuous guesswork on the part of the author, serving to bring the picture into accordance with the 1933 observations in terms of relative distribution of salinities. The salinity minimum south of Cuba (sal. 35.6–35.8‰) is, however, well defined by ample observations of surrounding salinities between 35.8 and 36.0‰ also in 1934.

With the apparent persistency of these relative distributions, it seems reasonable to conclude that local forces within the Caribbean region will generally tend to produce relative salinity minimums at the surface off the southwest coast of Cuba (between Cuba and the Caymans); another minimum south of Jamaica (and of the western part of Haiti ?); and a relative salinity maximum in the middle portion of the Central American bight which is continued along the north coast of South America to the eastward. The minima will probably be due chiefly to external factors, including land drainages from Cuba and Jamaica (and Haiti ?) and this will probably also be true of the minimum occurring immediately off the Central American coast (Panama to Honduras). But internal forces expressed in the slope of the water masses are probably mainly responsible for the surface salinity maximum particularly along the north coast of South America, while local evaporation may also be a contributory force especially in the Central American bight.

It will be noticed that the minima off Cuba and south of Jamaica, and the maximum in the Central American bight each occupy the location of one of the three main eddies indicated as probably being present in the surface circulation of the Caribbean (see figure 53, page 74). But this fact merely furnished us with an excellent illustration of the logical danger of drawing conclusions from such comparisons (see p. 77), since it is to a very considerable extent at least the very presence of these maxima, respectively minima, of surface salinity which causes the existence of these eddies to be indicated by depressions, respectively elevations, of the estimated dynamic topography of the surface. The latter are therefore not admissible as evidence in the explanation of the former, except to the extent that the depressions, respectively elevations, of the surface may be shown to have a deeper foundation in the underlying water masses inde-

pendent upon the conditions within the surface layer itself, for which the explanation is being sought. In other words, it is only in the dynamic topography of its lower limiting surface relative to deeper levels that we are logically entitled to look for an explanation of the features of the surface layer. For an intermediate layer one would want to consider both the upper limiting surface in relation to the actual sea surface, and the lower limiting surface in relation to some deeper datum level, leaving the layer to be studied out of both calculations. But for the surface layer itself, the field of energy of the upper limiting surface thus understood would be expressed by meteorological and not by oceanographic forces. As shown in figure 49 and mentioned on page 72, the eddy-generating factors are only very faintly defined in the dynamic topography of the 200 decibar surface relative to the 600 decibar surface, and it therefore seems as though there is only at best a very slight degree of independence between the maxima and minima in the surface layer and the elevations and depressions of the surface topography in this instance.

In our presentation of distributions in horizontal perspective below the surface layer, we shall outline the occurrence of the main types of water masses identified by the temperature-salinity correlation method (see pp. 77–89) regardless of depth, according to the method already used in our previous report on the Gulf of Mexico (Parr, 1935, figure 8, p. 20) and further argued by Wüst (1936, p. 133). Figure 41 thus shows the distribution of maximum and figure 42 the distribution of minimum salinities.

In the latter figure corresponding hatchings have been broken, and the contour lines dotted in the areas in which the distribution of minimum salinities have been determined on the basis of the 1934 observations alone, with the possibility of a discrepancy with the 1933 data, since the smoother contour lines which could patently have been drawn on the basis of the 1933 observations taken by themselves might suggest the possibility of an actual difference between the two years in regard to distribution of minimum salinities. This particularly applies to the high minimum salinity value observed in the Central American bight in 1934, although these higher values ($35.80–35.85^{0}/_{00}$) do perhaps also break through the 1933 profile from Colombia to Mesquito Bank, but in any event only over a disproportionately narrow distance. It is, of course, also possible that we may have an isolated patch of high minimum salinity values in the

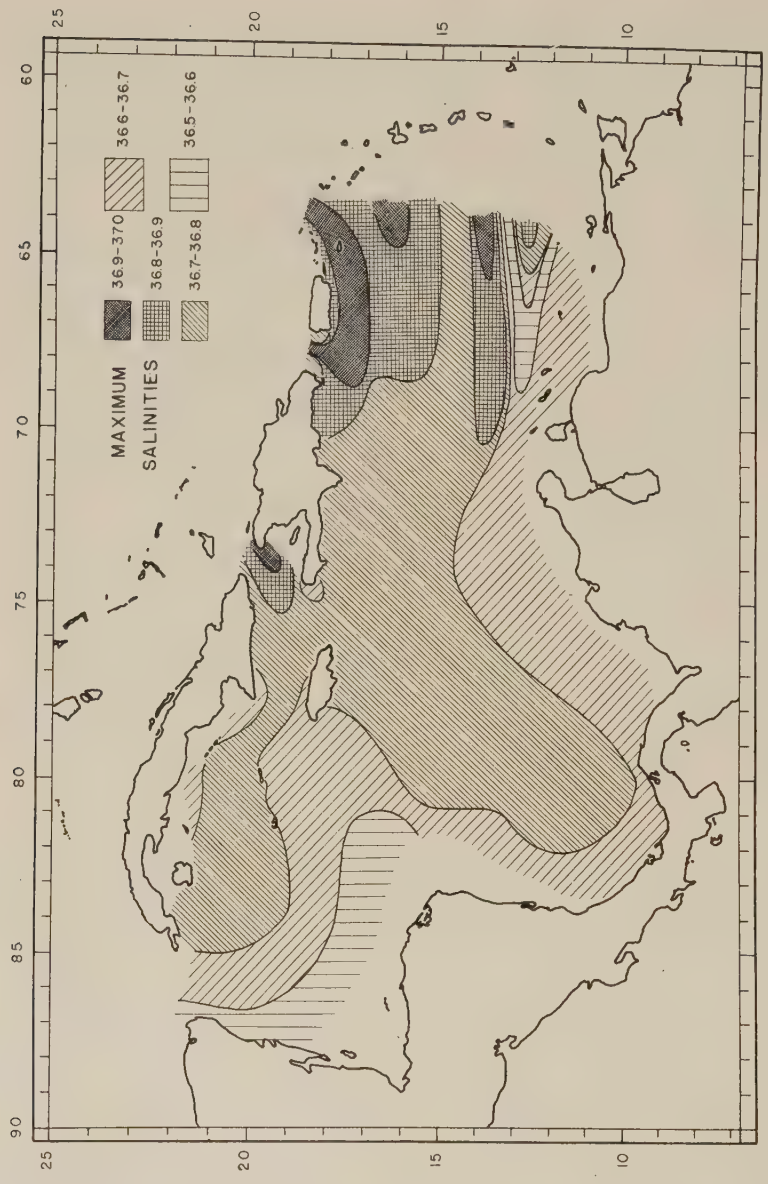

Fig. 41. Distribution of maximum salinities. Observations from 1933 and 1934 combined.

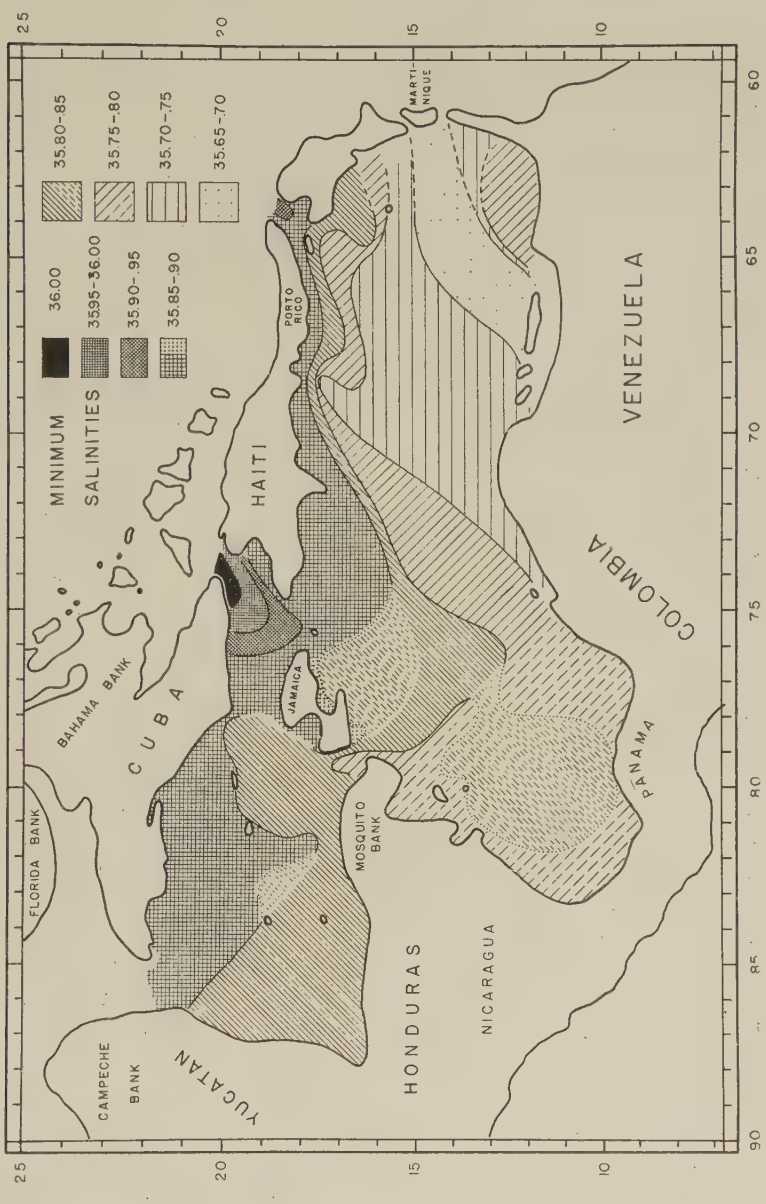

Fig. 42 Distribution of minimum salinities. Observations from 1933 and 1934 combined.

Central American bight, and perhaps this should even be considered the most likely explanation of the picture.

When we take into consideration that the general increase in minimum salinities, and decrease in maximum salinities from East to West and Northwest is due to progressive mixing between the sub- and superjacent water masses around the minimum and maximum salinity sheets, a comparison of figures 40 and 41 particularly in the eastern Caribbean clearly shows a predominance of northern influence in the maximum salinity layer and of eastern and southeastern inflow in the minimum layer. This is entirely in accordance with our deductions from the temperature-salinity correlation curves (page 82) from which we conclude with Nielsen that the maximum salinity layer must be mainly derived from the southern Sargasso Sea (Jacobsen's area VI) and the minimum salinity layer from the tropical Atlantic (Jacobsen's area XIV).

It will also be seen from figures 41 and 42 that the streakiness of the maximum and minimum salinity layers at the eastern end of the Caribbean, which is undoubtedly in both cases due to separate origins of the various streaks through different passages between the Antillean island, with different degrees of mixing influences in each, has entirely disappeared at about 70° Western longitude, and only a comparatively uniform gradient remains to the westward.

Since the disturbing influence of progressive mixing between sub- and superjacent water masses should be completely eliminated in the rectilinear portion of the temperature-salinity correlation curves, between the curvatures around maximum and minimum values, the author conceived of the possibility of obtaining a perhaps even clearer picture of horizontal distribution in the intermediate layer, in spite of the much smaller differences with which one would there have to deal. Accordingly the intercepts between the coordinate for 15° C. and the temperature-salinity correlation curves, which fall approximately at the center of the straight portion of the latter (see figures 58–82) were chosen as a basis for plotting the horizontal distribution of salinities in the 15° isothermal sheet. This method of analysis proved successful beyond expectations.

In figure 43 salinities at 15° C. are plotted against distance for the three North-South profiles through the Eastern Caribbean, and for the Southeast portion of the Southeast-Northwest profile across the Central American bight made during 1933 (see figure 1, p. 3). This

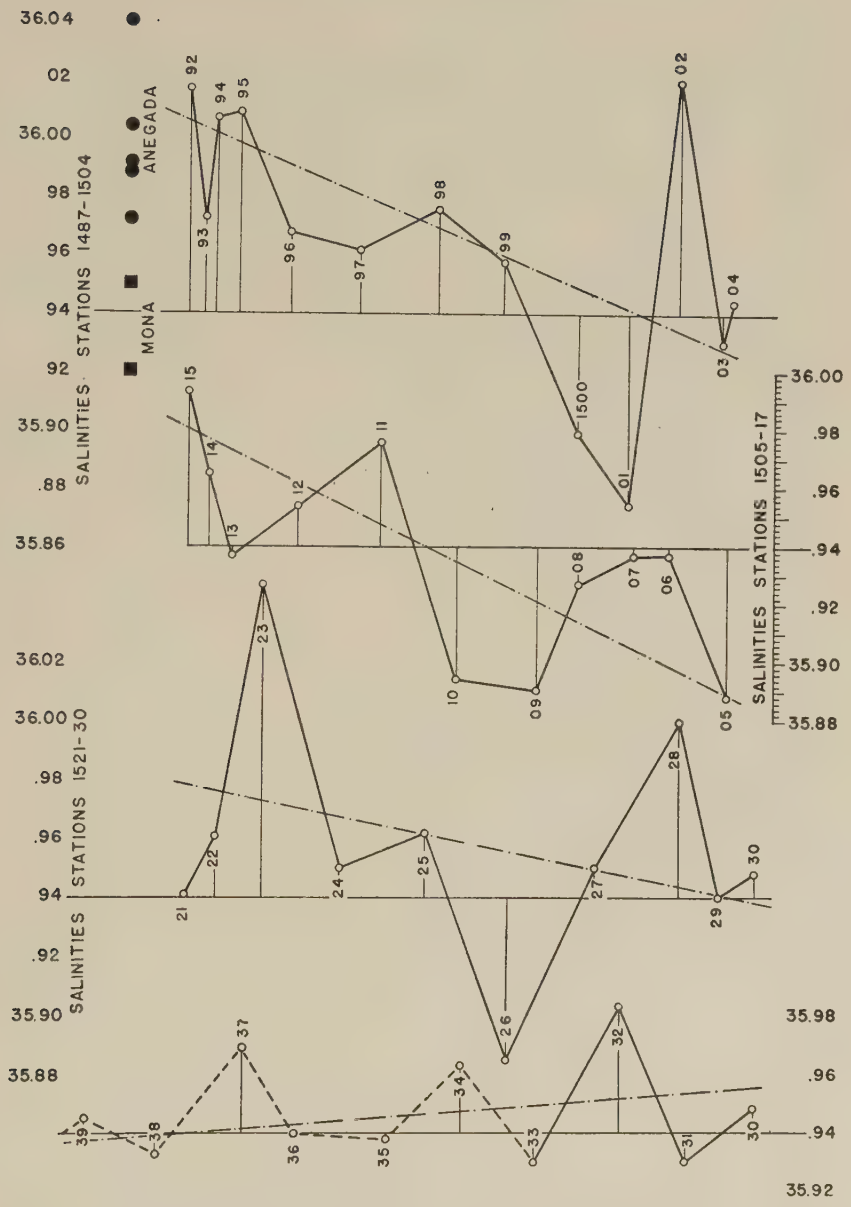

Fig. 43. Salinities at 15° C. temperature in the North-South profiles through the eastern Caribbean from 1933. Scale given for St. 1505–17 can be used to measure from base lines (35.94 ‰) of each curve. Salinities in Anegada Passage (black surface) are referred to the base line for St. 1487–1504. Salinities in Mona Passage (black squares) to the base line for St. 1505–1517.

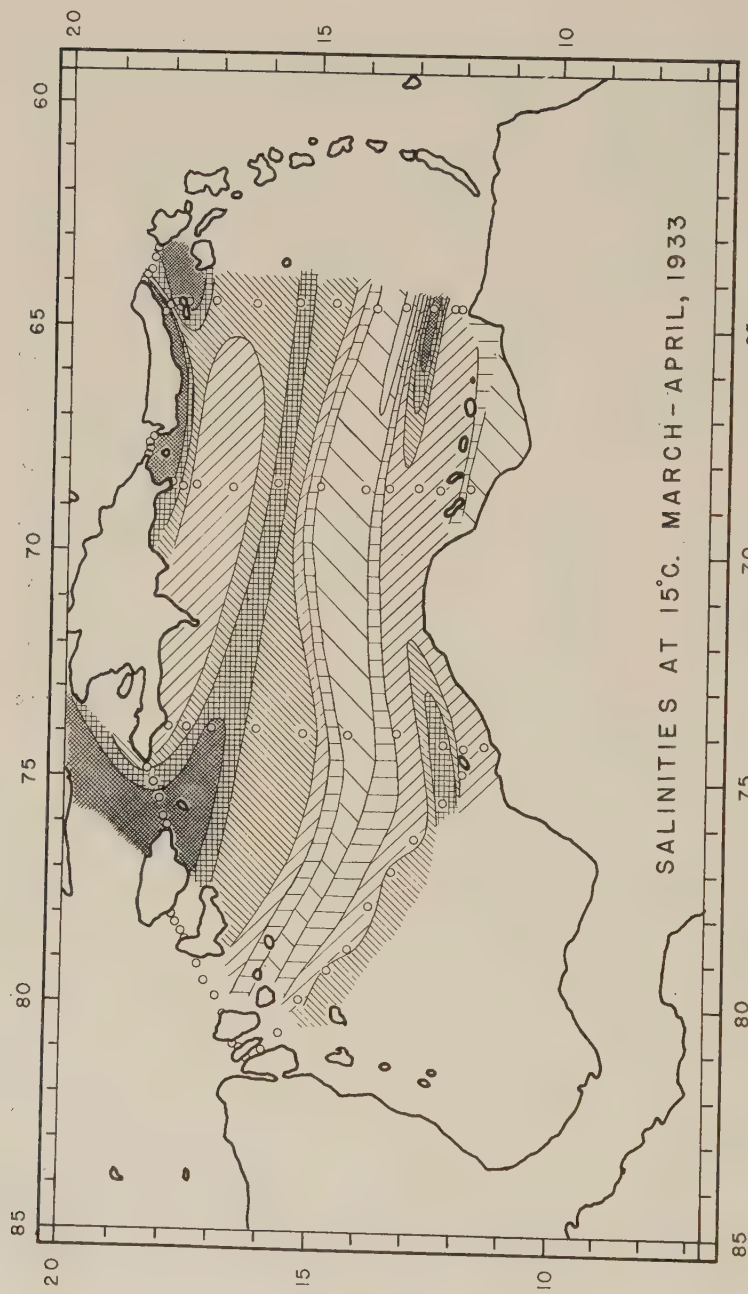

Fig. 44. Salinities of 15° C. isothermal surface in March to April, 1933. Curves and hatchings for every 0.02‰ salinity from < 35.88 to > 36.00‰.

illustration shows an apparent consistency of modes and valleys through all three of the N-S profiles. All the three curves show a valley immediately off the north coast of South America followed by a well-marked mode, north of which we again find another deep valley. The next mode and valley north of this central valley are also both very distinct, although a minor irregularity in the form of a shoulder appears on the south side of the mode in the third profile. Our most Eastern profile (at the top of the figure) ends in a high mode in the North broken only by an irregular depression in the narrow channel between St. Thomas and St. Croix. This Northern mode has narrowed and diminished in our second profile and is totally absent in the third. If these data are combined in a presentation in horizontal perspective as done in our chart, figure 44, we see that they give a perfectly rational and surprisingly consistent picture. The outstanding feature of this picture is the apparent persistency of the streakiness of the 15° C. isothermal sheet in comparison with the streakiness of the maximum salinity layer, above, and the minimum salinity, below, both of which developed a uniform gradient already at about 70° Western longitude, as above mentioned. From figure 45, showing the average temperature-salinity correlation curve for this region (represented by our second N-S profile, St. 1505–1515, see figure 62) it is evident that the 15° C. isothermal sheet represents the layer of minimum vertical stability, while both the maximum and the minimum salinity layer represent separate maxima of vertical stability. The theoretical implications of this relationship will be discussed more extensively in a separate article (Parr 1936a), and it will suffice for the present merely to say that it points to the conclusion that vertical stability not only reduces vertical mixing but actually increases lateral mixing as well, in accordance with obvious expectations on the basis of certain elementary considerations.

Only when the waters in their westward flow reach the complicated topographical region of the banks between Honduras and Jamaica does it finally become impossible to trace the individual streaks of the 15° C. isothermal sheet any further, although a streakiness still remains. The lapse of time between the 1933 and the 1934 observations also proves to have raised similar obstacles against a combination of the data for the two years in their finer details. If, however, we confine ourselves to a consideration only of the rectilinear trends of salinities in the 15° C. isothermal sheet, all our observations for both

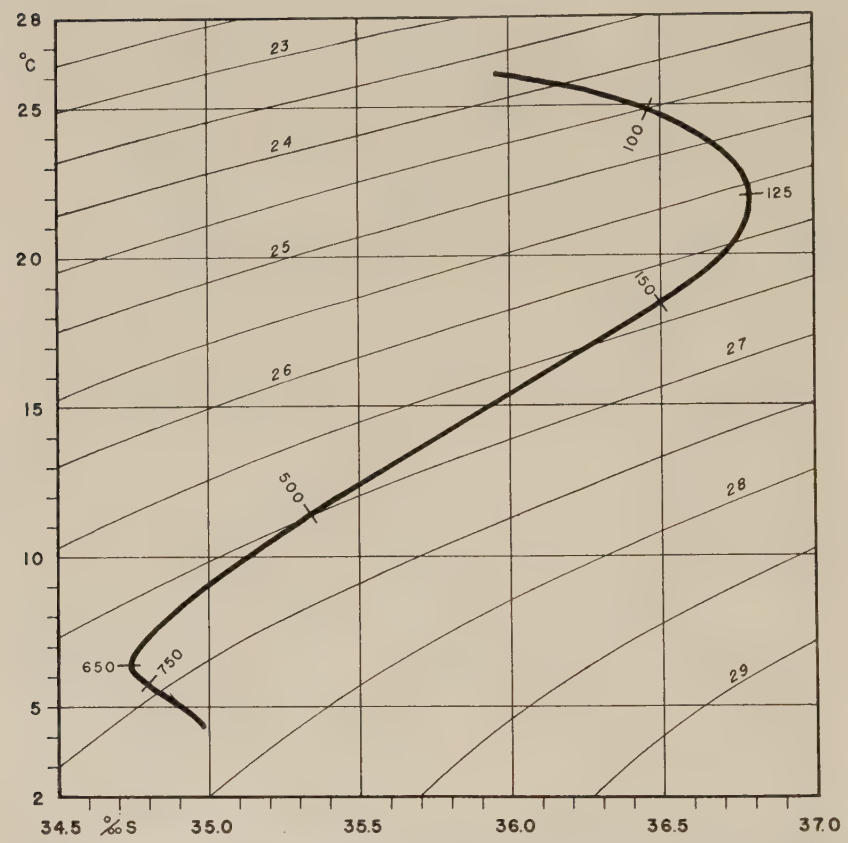

Fig. 45. Average Temperature-Salinity correlation curve for second North-South profile (St. 1505–1515) with selected approximate average depths, and with isopycnals entered for every 0.5×10^{-3} specific gravity (δ_t).

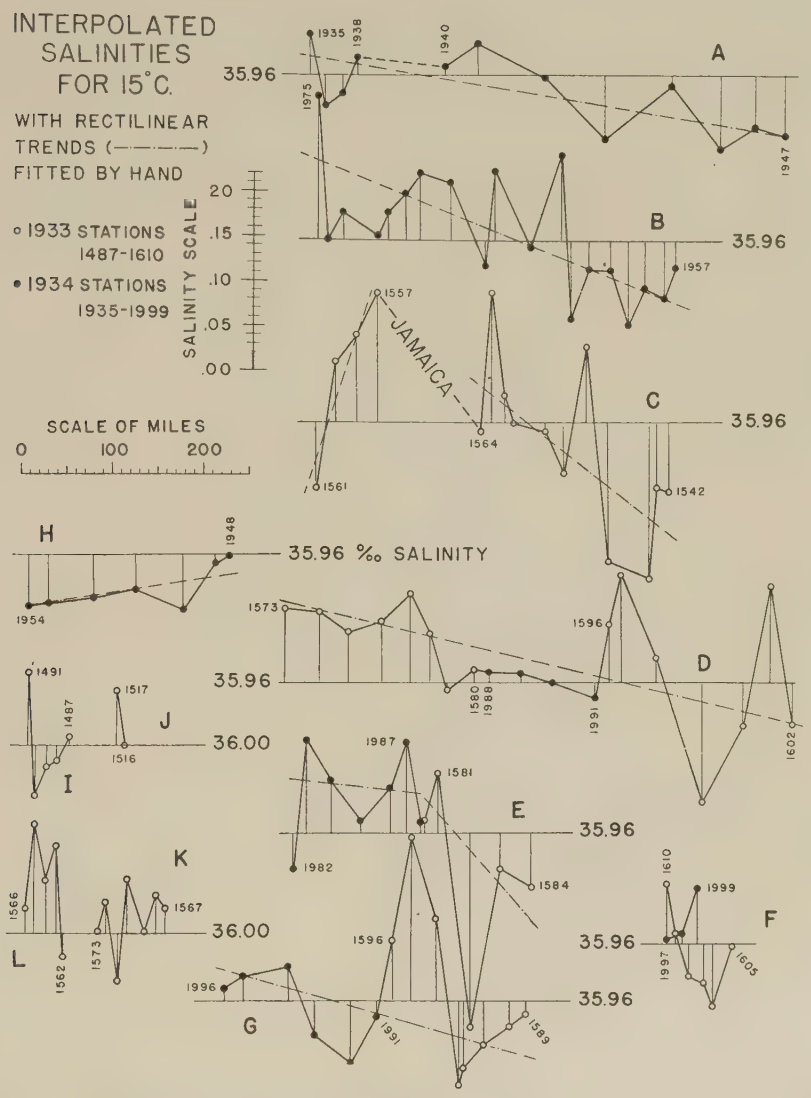

Fig. 46. Salinities at 15° C. temperature in all profiles except those shown in fig. 43. With rectilinear trends fitted by hand.

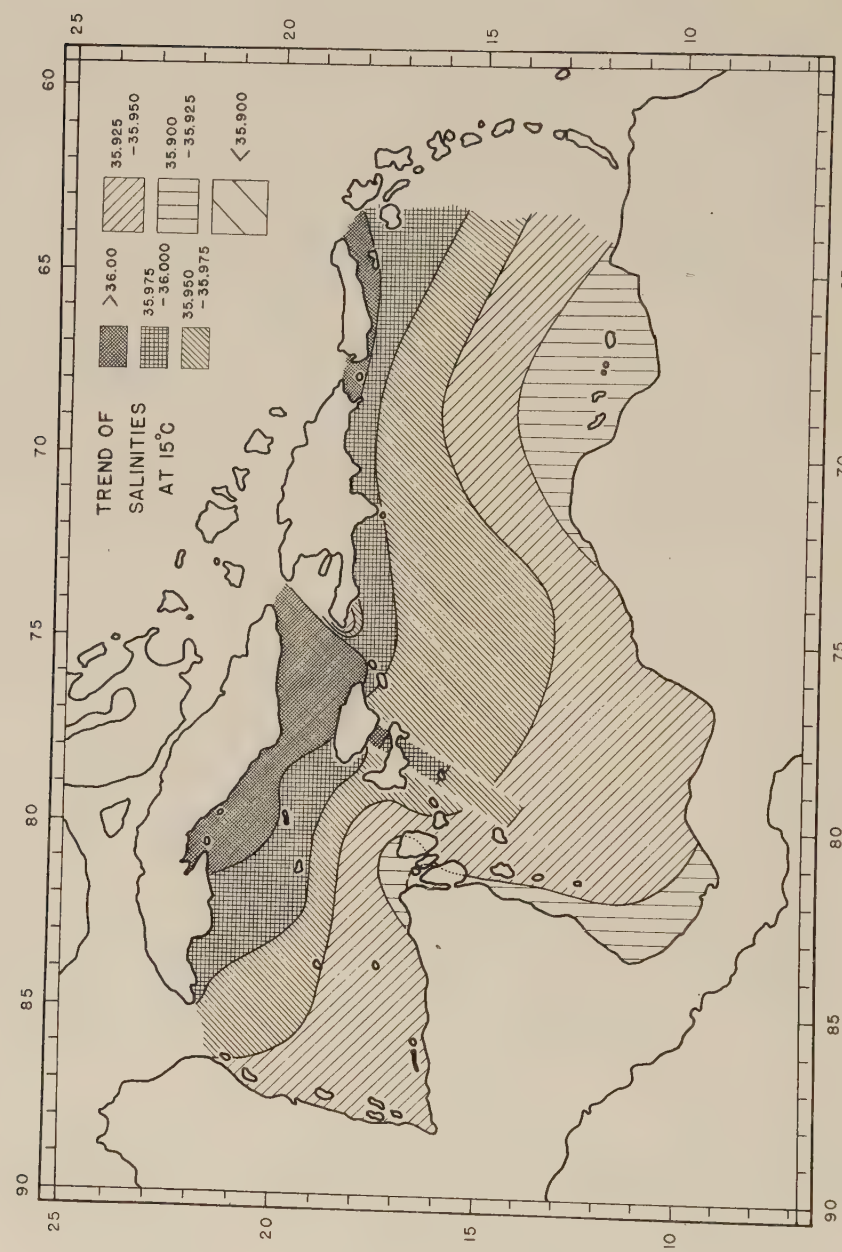

Fig. 47. General trend of salinities in 15° C. isothermals sheet. Observations from 1933 and 1934 combined. Deviating values observed in part of one series from 1934 shown as an insertion southwest from Jamaica.

years fit together very nicely to form a single harmonious and rational picture with the only exception of the data from a part of one of the 1934 profiles (Stations 1964–75) southwest of Jamaica, which shows discrepantly high values, as indicated in our figure 47. Figures 46 and 43 on page 61 together present all the data and lines of trend fitted by hand, used in the preparation of our chart (figure 47). In fitting the lines of trend the individual interpolations have to a certain extent been evaluated by their probable accuracy depending upon the distance between the 15° C. intercept on the temperature-salinity correlation curve and the nearest actual observation, and by similar considerations. That is to say, a deviating value obtained by interpolation over a relatively wide range has been given less attention than a value almost directly taken from actual observations. In any event, it is clear that no difference of subjective preference in the precise details of fitting the trends can alter the direction or even the fundamental magnitude of the slopes to any significant extent.

From our figure 47 it would appear as though the Caribbean waters must have originated mainly from the East and Southeast (Jacobsen's area XIV) already at the depth of the 15° C. isothermal sheet (see figure 35), and that the intrusion of the maximum salinity water from the southern part of the Sargasso Sea must in consequence be mainly limited to *less* than the depth between the surface layer and the 15° C. isothermal sheet (see figure 35, page 46).

GENERAL CIRCULATION

For the purposes of this report our consideration of dynamics will be limited to a presentation and general interpretation of dynamic topographies, while current profiles, energy and velocity calculations are being reserved for special treatment in a separate publication.

The dynamic topographies are presented in three depth integrals (figures 48–50): 0–200; 200–600; and 600–1200 decibars; and their integration is shown in the final chart giving the dynamic topography of the surface in relation to 1200 decibars (figure 51).

By far the greatest differences of relative dynamic heights are found in the first integral (0–200 decibars), covering a total range from less than 40 (35–40) in the extreme Southeast to more than 75 dynamic centimeters anomaly in the North. If the exceptionally high value obtained at the single station (1939) south of Jamaica in 1934 is included the upper limit is thereby raised to more than 85 dyn. cm.

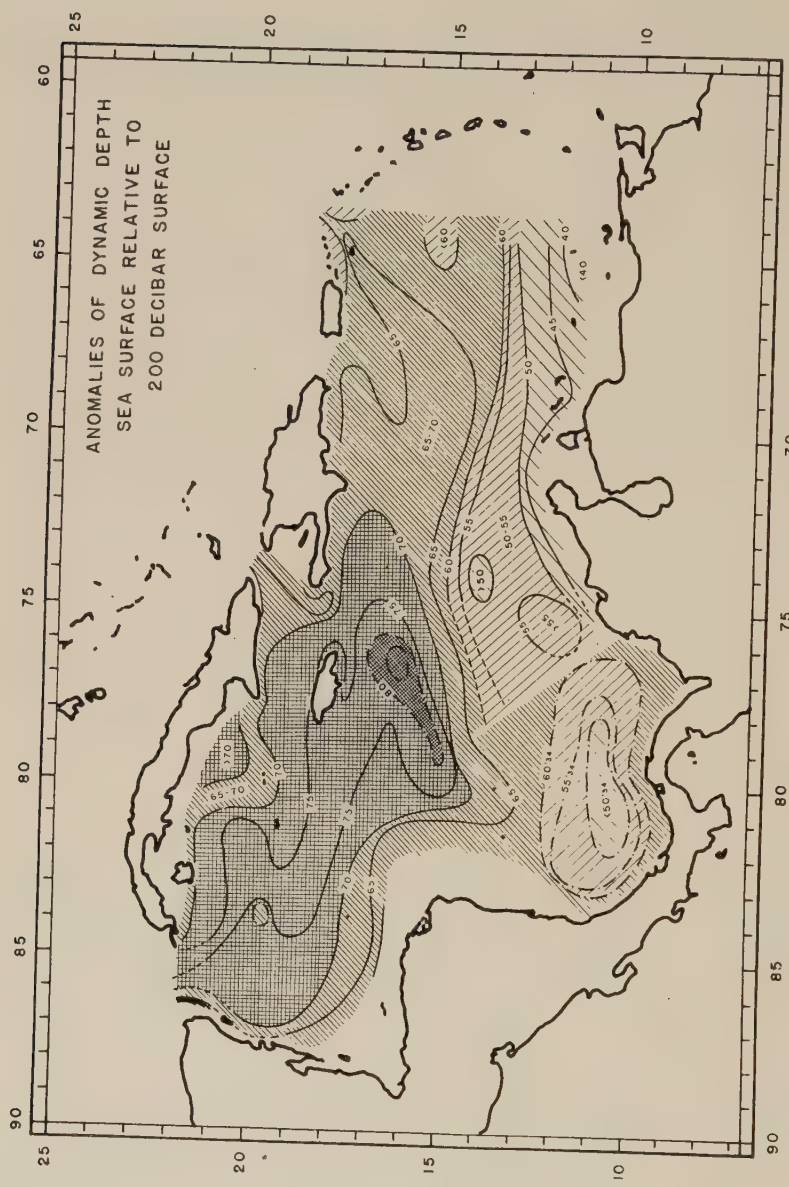

Fig. 48. Dynamic topography of surface relative to 200 decibars.

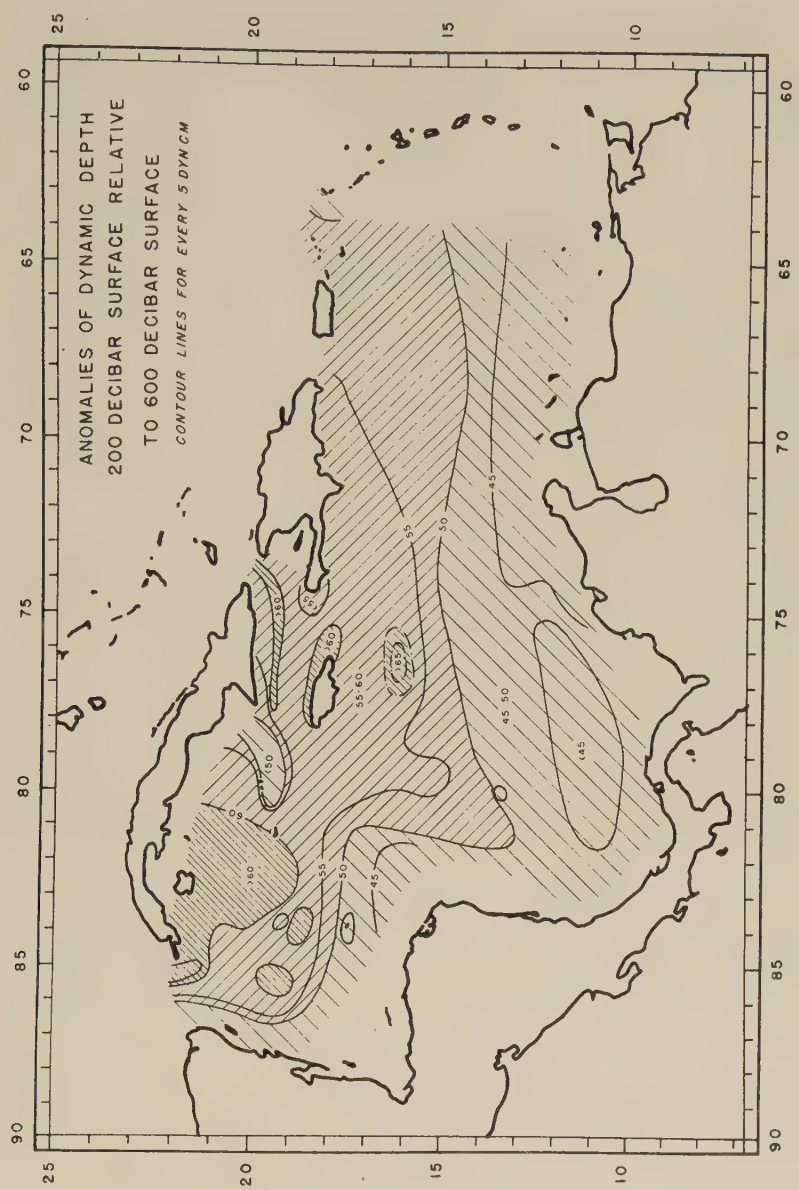

Fig. 49. Dynamic topography of 200 decibars relative to 600 decibars.

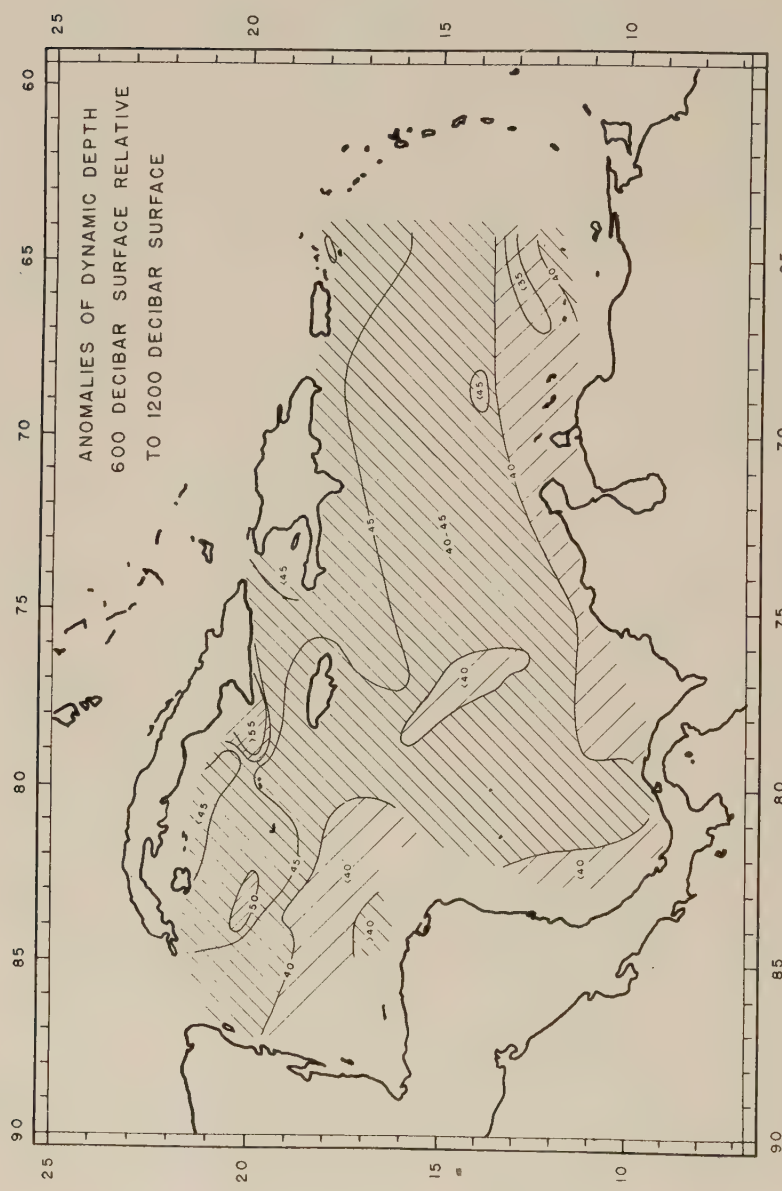

Fig. 50. Dynamic topography of 600 decibar surface relative to 1200 decibars.

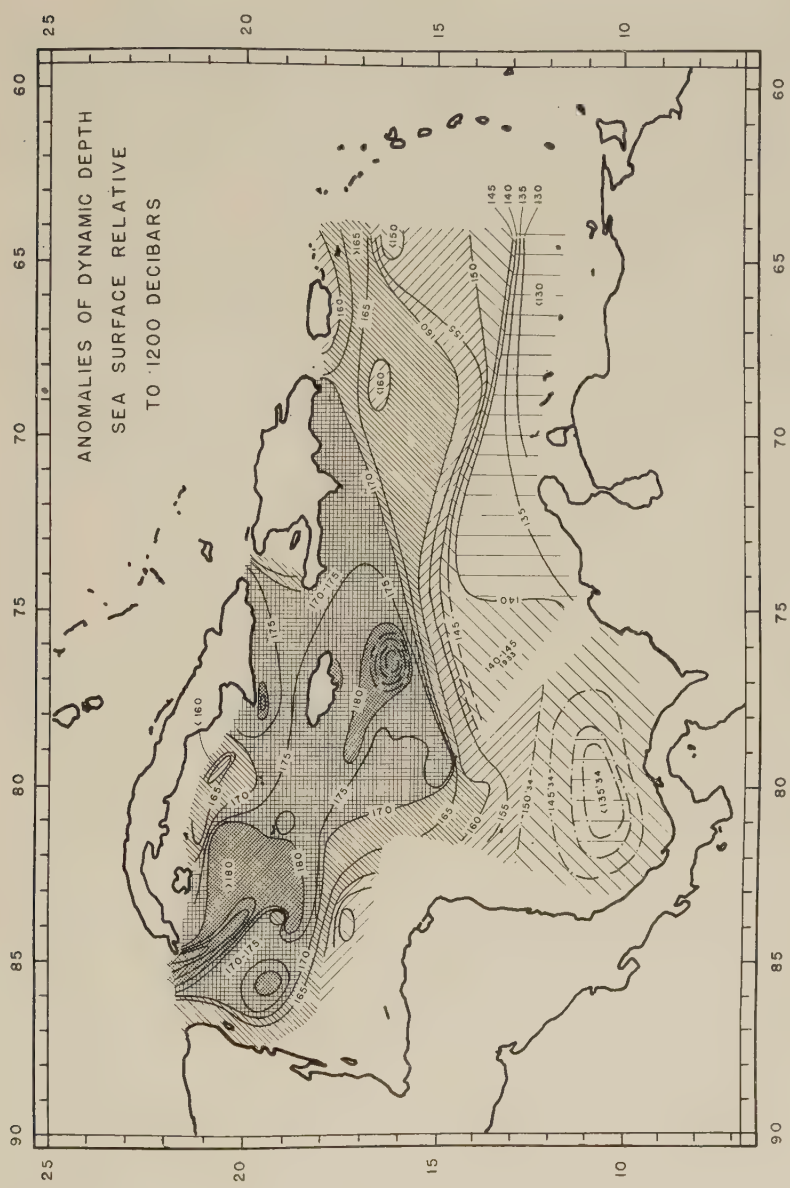

Fig. 51. Dynamic topography of surface relative to 1200 decibars.

Although we are dealing with twice the thickness of water, the entire range between 200 and 600 decibars is only about 20 dyn. cm., from less than 45 (40–45) to less than 65 dyn. cm. anomaly (or to less than 70 dyn. cm. when the single exceptional station south of Jamaica is included). From 600 to 1200 decibars, where we have three times the thickness of our first depth integral the range is also only about 30 dyn. cm. from <35 to <60 dyn. cm.

While the dynamic gradients are thus rapidly decreasing in the lower depth integrals, all three integrals are in good agreement with each other in regard to all general features in the horizontal distribution of relative dynamic heights, showing no change to a significantly different circulation pattern at any level between the surface and 1200 decibars, with the exception that a counter-current (reversal of gradient) occurs conspicuously at the southern end of our most eastern cross-section. Similar counter-currents in the West and South are also calculated in the Yucatan channel and at other points but do not appear sufficiently conspicuously in the combined dynamic topography of the two years 1933 and 1934 for the particularly depth integrals here selected, to be shown in the illustrations.

With this agreement between all integrals we may take the dynamic topography of the surface relative to 1200 decibars as a generalized illustration of the entire circulation system contained between these levels, and it is furthermore evident that by far the fastest and most significant flow occurs in the integral between the surface and 200 decibars alone.

On two points the observations from 1933 and 1934 have proved difficult to combine directly and they thereby give absolute evidence of variations in the hydrography of the Central American seas between these two years. In the triangle Jamaica-Honduras-Colombia the observations from 1934 give generally higher values of relative dynamic heights than those indicated in the observations from 1933, beginning with an exceptionally high value obtained at the previously mentioned single station (1939) in the center of the eddy region south of Jamaica, and continuing with such high values south of the 1933 profile from Colombia to Honduras (st. 1531–45, see figure 1) that it is impossible to combine the picture of conditions in the southwest area towards Panama in 1934 with the observations made in adjacent waters in 1933. But if we compare the 1933 profile of relative dynamic topography of the surface from Haiti to Colombia (st. 1521–1530)

extrapolated along indicated contour lines to the Jamaica-Panama line, with the observations made along the latter profile in 1934, as shown in figure 52, we find an excellent agreement in main features underlying the differences in accurate values developed between the two years. In both years we find a definite elevation of dynamic topography south of Jamaica, indicating eddy movements in this

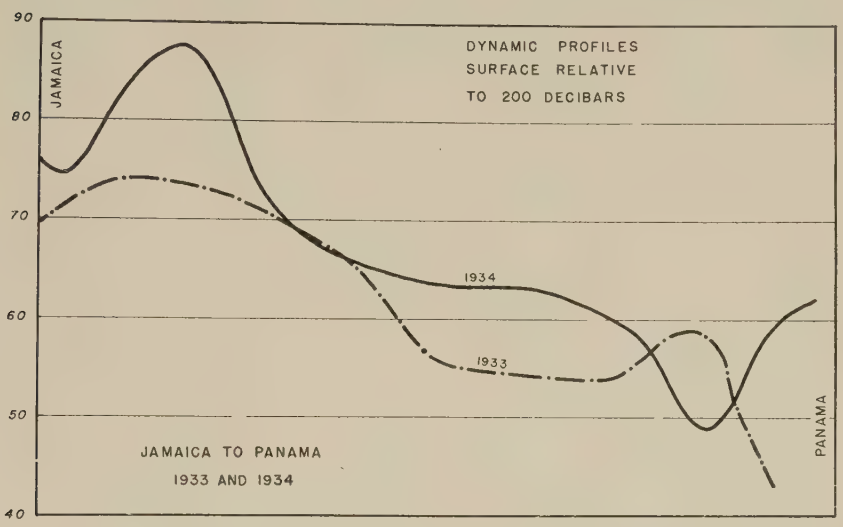

Fig. 52. Dynamic profile of surface relative to 200 decibars from Jamaica to Panama in 1934 with exterpolations to same line along probable contours from observations between Haiti and Colombia and from Colombia towards Honduras in 1933.

region; followed by a sharp decline, indicating the path of the main current. South of the main current both profiles show a wide, almost level stretch of nearly quiescent waters, beyond which eddies in opposite directions are indicated. When plotted in horizontal distribution (figure 48) it will be seen that these eddies in opposite directions in the south are not in conflict, but leave ample room for each other.

We also find some differences in dynamic topographies in the Yucatan Channel when two years are compared, but these will be treated more fully in the separate report on dynamics now in preparation.

Extracting from these dynamic topographies the main features of the horizontal circulation in the Caribbean and Cayman seas we ob-

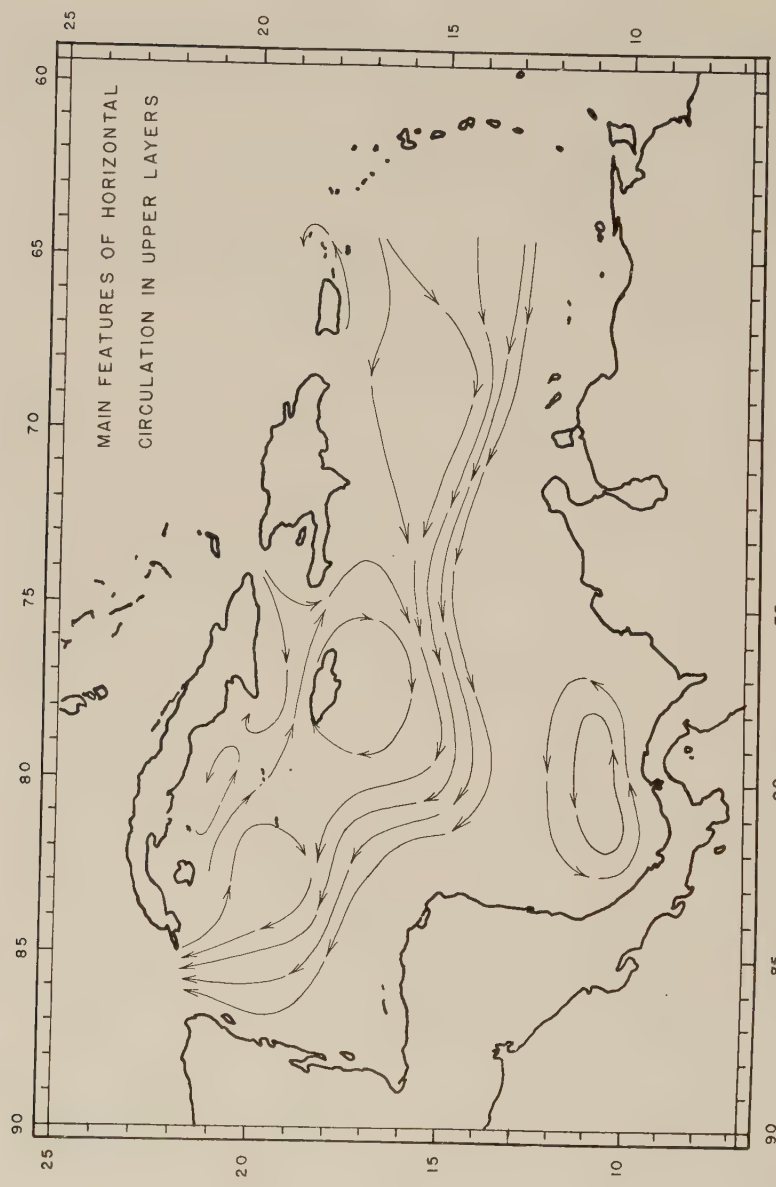

Fig. 53. Probable general features of horizontal circulations in the upper layers of the Caribbean and Cayman seas.

tain the picture shown in figure 53; with the main flow starting from the southeast rising towards the middle of the Caribbean, and undulating with the topography of the western shore to the Yucatan Channel. South of this main flow we have a large eddy in the Panamanian bight between Honduras and Colombia. North of the main flow we have a similar large eddy south of Jamaica, and a more complex system of eddies and counter-currents between Cayman Island and Cuba, apparently sending an arm down along the north coast of Jamaica to join the main flow in the Caribbean, together with a branch from the inflow through the Windward Passage, after circumventing the eddy south of Jamaica.

With due consideration of all the restrictions inherent in the interpretation of dynamic topographies, these simple main features can probably be taken to give in gross approximation a correct representation of the general circulation in the Central American seas; while the final details must be left for the special report on dynamics.

Before concluding our discussion of dynamic topographies, however, it may be of interest to point out that regardless of how one might choose to interpret the exact path of the main current it *must ascend a considerable calculated dynamic slope* to pass from the eastern end of the Caribbean to the Yucatan Channel.[1] As the path has been plotted in figure 53 the ascent would be from an average anomally of dynamic height at the surface relative to 1200 decibars of only about 140 dynamic centimeters in the southeast to an average of about 170 dyn. cm. in the Yucatan Channel. While external forces in the form of changes in specific volume caused by heating (Parr, 1936b) may contribute a little to this increased elevation, other explanations must be sought to account for the major part of the rising dynamic height in the longitudinal direction of the current in this instance. A separate article on this problem is now in preparation.

BOTTOM CIRCULATION

The relationship between the Central American bottom waters and the Atlantic waters outside at threshold level provides an interesting and important mechanism of inflow reversing the relationship between the North Atlantic and the Norwegian Sea. As we have

[1] Due to the uniformity of the deeper layers inequalities in the 1200 decibar surface sufficient to compensate for the calculated increase in dynamic thickness above can not be derived from the observational data by standard methods of computation.

seen already (p. 50), the salinities inside of the Caribbean remain constant to the bottom from about 1500 meters depth and the same would appear to be true over a considerable depth around threshold level also outside. But outside temperatures continue to decrease downward while inside temperatures remain almost the same at all levels below threshold depth. In consequence the inside bottom waters are always of less specific gravity than the outside waters normally extending below the threshold depth in the Atlantic. As a result, the slightest rise in the layers of Atlantic waters outside, or the slightest longitudinal drop in the temperature of these outside waters as they flow by the various passages to the Caribbean, must cause an immediate cascading of Atlantic water into the bottom of the Central American basin. That there would generally be a sufficient amount of variation in outside conditions to keep this inflow mechanism in fairly regular operation would probably be taken for granted. We furthermore have actual observations from three separate sources tending to confirm this assumption.

On one hand we have the low temperatures observed at Station 1493 which give at least one instance of water heavier and colder than any normal bottom water of the Caribbean already inside the threshold in a locality from which it must therefore continue to sink further into the Central American basin along the ocean bottom.

On the other hand, we find that when we correct for adiabatic heating there actually is a slight but appreciable decrease in temperatures from the threshold level down to the deepest bottom in the Central American basin (see figure 37, p. 49), suggestive of variations in threshold temperature and evidence of an inflow along the bottom. Finally the fact that the deepest bottom waters of the Caribbean basin have proved to be very rich in oxygen (Seiwell: MS) shows that these bottom waters are not stagnant, and furthermore suggest that the deepest layers are also the freshest with regard to this feature.

If conditions on both sides of the threshold were permanently stable, water would only flow in over the threshold to compensate for the water masses which might be drawn into the outflow from higher levels by friction against the upper currents (Rossby 1936), and this inflow should then be expected to follow a horizontal level, not the bottom, since a permanent static equilibrium at the threshold would provide no force to drive the water downward and the compensation requirement would develop mainly at the higher level. This would

leave the bottom waters of the Central American basins stagnant below threshold level, and the fact that this is not found to be the case as well as the other considerations above mentioned would therefore seem to be definite evidence of the operation of the inflow mechanism above suggested.

But when outside variations cause a fresh inflow over the threshold, this inflow must create an upward-lifting force underneath the entire Caribbean water masses. This uplift from the bottom must thus add itself to the other forces propelling water out of the Central American seas at higher levels. In an open ocean, e.g. by a bottom overflow from the Norwegian Sea into the North Atlantic, this effect would undoubtedly be quite insignificant, but in such enclosed basins with narrow outlets as those of the Caribbean region it might conceivably require quantitative consideration, although the high normal volume rate of flow of the Caribbean surface current would of course reduce the relative effect of this uplifting tendency.

We thus see the Caribbean bottom water entering along or near the bottom becoming gradually heated by mixing with the superjacent water masses, and also at first undergoing an adiabatic heating, subsequently followed by adiabatic cooling as it is gradually pushed upward again by fresh bottom inflow, to be ultimately carried away by friction in the higher current system.

CHARACTERISTICS, ORIGINS AND RELATIONSHIPS OF WATER MASSES

The chief means of defining the characteristics of the various water masses and of studying their origins and relationships is found in Temperature-Salinity Correlation Method first introduced by Helland-Hansen. Further evidence may be looked for in a study of horizontal distributions and of the calculated dynamic features of the region considered, and in a comparison between the results obtained by these two methods of approach. When making comparisons between horizontal distribution and calculated dynamic topography, one must not lose sight of the fact that this is not a comparison between different and independent statistics, but merely between different elaborations of the identical primary data. A rational agreement between dynamic topography and horizontal distribution is therefore actually only suggestive of a possibility of a causal relationship between the two, but

is in no sense whatever to be regarded as logical evidence of the actual existence of such a relationship without further analysis. This point has been further elaborated on page 56.

Figures 58–82, pp. 93–110, show the Temperature-Salinity correlation curves for the various stations in the Caribbean in geographical rather than chronological order, each illustration representing a separate profile or part of a profile which may be located by comparing its legend and station numbers with the map given in figure 1 on page 3. A cursory glance through these illustrations immediately reveals the fact that the variations of practically all individual station curves are merely in the nature of minor modifications of an identical fundamental pattern, which we may call the Caribbean pattern, and that we are thus throughout this entire region dealing with a singularly closely related system of water masses. It might be mentioned at once that the few conspicuous deviations from this general pattern brought to light in the course of these investigations were all observed on or near the left side of the main direction of surface flow (from East to West and Northwest), that is, in the neighborhood of the South and Central American coast forming the Southern and Western boundaries of the Caribbean and Cayman Seas. Apart from these few exceptions, which will be given separate attention later, we are then at this point chiefly concerned with the story told by the individual modification of the Caribbean Temperature-Salinity correlation pattern observed at the single stations. While these modifications in some instances would seem to retain their individual identity over surprisingly long distances of flow, the modifications in other cases show an orderly and gradual progression in the direction of the main current. Since the significance of the individual modification can obviously only be interpreted through their relationship to this orderly progression, it is in this instance advisable to proceed from the general to the particular. We shall therefore begin with the comparison of average[1] temperature-salinity correlation curves for the main series of transverse profiles across the Central American basins as shown in figure 55.

In this figure the average curves have been numbered according to

[1] Determined by interpolations to standard temperatures on the individual station curves for temperatures of 10° C. or higher, and by average correlation of actual observations below 10° C. (Without weighting of the data. See Parr 1935, pp. 34–41.)

the geographical sequence of the profiles they represent, counted in the direction of the main flow from East to West and Northwest, and it is immediately obvious that this picture, based on the 1933 observa-

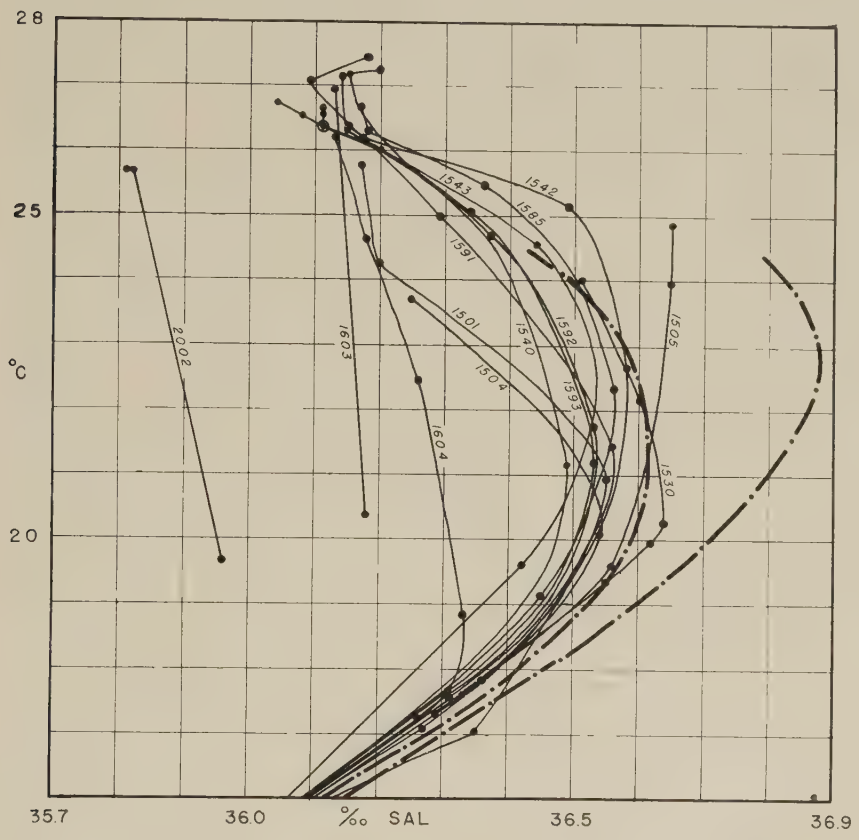

Fig. 54. Upper portions of deviating Temperature-Salinity correlation curves from left side of direction of main flow. Portions of average curves I and V in figures 55 entered in heavy dot and dash for comparison.

tions, gives a beautiful illustration of progressive mixing between the water layers around maximum salinity in the course of the westward movement. We see the point of inflection withdrawing farther and farther from its maximum value in the East and we also observe how the rate of this withdrawal per unit geographical distance decreases

as the arc of the curve around maximum salinity broadens in consequence of the mixing itself. It is perfectly obvious, of course, that geographical distance is in no manner a reliable index of progression

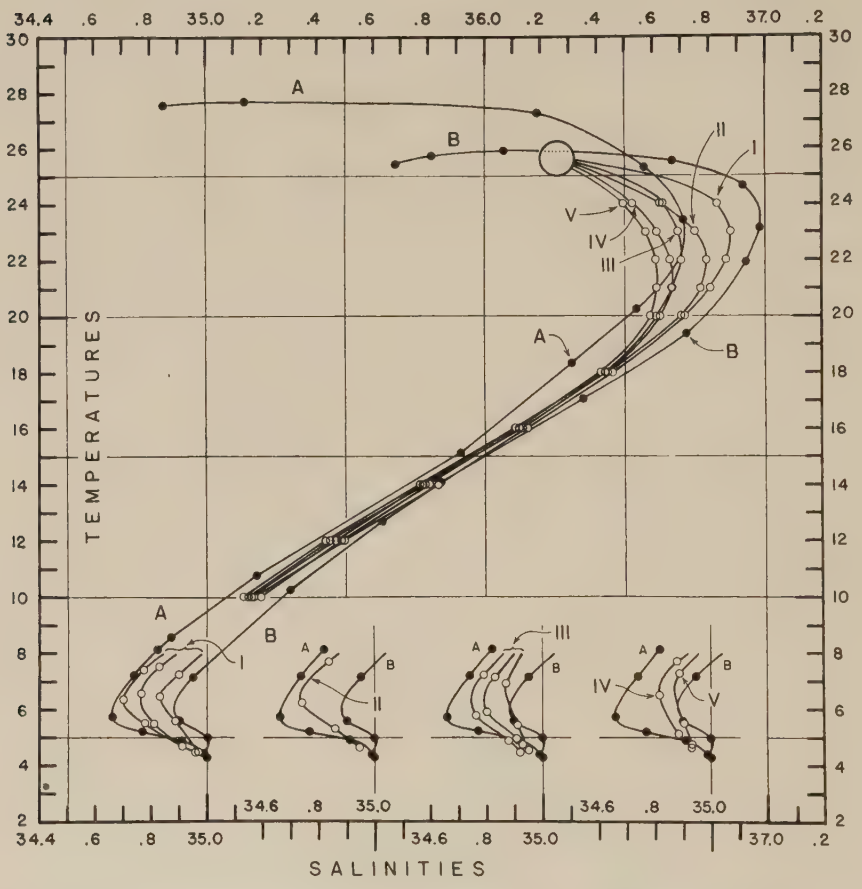

Fig. 55. Average temperature-salinity correlation curve for 1933 profiles of Caribbean Sea and Yucatan Channel. With group averages for each profile around minimum salinities shown separately at bottom with average curves for Jacobsen's area VI (curve B) and XIV (curve A).

of mixing and of mean flow in accurate terms, there being too many variables and uncertainties involved in regard to speed of current and intensity of turbulence. Nevertheless the rational reduction in

the rate of withdrawal from maximum salinity values seems worth mentioning as another feature illustrated in gross approximation in this figure.[1]

In 1934 it would appear as though the mixing had progressed slightly slower than in 1933 as indicated by the fact that the average curve for the two profiles[2] geographically located between profiles III and IV, fall between the averages for 1933 profiles II and III below 23° C., and between III and I above 23° C. around maximum salinity (see figure 54). It is quite in accordance with this difference between the two years in the waters south of Jamaica that the Yucatan Channel profile also gives a higher average maximum salinity in 1934[3] than in 1933 (see figures 81 and 82, pp. 109–10) but the orderly progression is seen also in the 1934 records, and the difference from the observations from 1933 is not sufficient to change the fundamental pattern of progression shown in the more complete series of profiles obtained in that year.

In regard to minimum salinities, the station curves, particularly in profiles I and III, apparently fall into such definite groups that it has not been considered advisable to present them by a single average for the entire profiles but by group-averages instead. In spite of this lack of uniformity, the progressive withdrawal of the inflection point from minimum values is no less evident than the withdrawal from maximum values in the upper portions of the curves.

It is of course an obvious and generally accepted fact that the Caribbean must receive its water masses mainly at its eastern end through the various passages between the Lesser Antilles from the Virgin Islands to Trinidad. Some further contributions may also be received through the Mona Passage, between Porto Rico and Haiti, and through the Windward Passage between Haiti and Cuba. The assumption of a chiefly eastern entry is entirely borne out by the fact that it is in the most eastern profile (I) that the average temperature-salinity correlation curve takes the form indicative of the least

[1] The average geographical distances between the profiles as numbered in figure 55 actually increase somewhat in the sequence indicated by these numbers in the following manner: distance I–II about 230 nautical miles; II–III about 310 nautical miles; III–IV about 350 n. mi. (between midpoints); IV–V about 430 n. mi.

[2] The averages of these two profiles (Stations 1935–1947 and 1964–1975, see figures 64, 65 and 67, pp. 98–9) do not differ significantly from each other at all.

[3] Following approximately 1933 profile IV, instead of V.

advanced stage of mixing between super- and subjacent water masses, with the highest maximum and with the lowest minimum values.

This curve can therefore best be taken to illustrate the character of the major part of the Caribbean water masses immediately after they have made their entrance into the Central American seas, and it becomes of interest to compare the curve of profile I in particular, with the average temperature-salinity curves for the Atlantic waters outside. Such curves have been presented by Jacobsen (1929) and in figure 55 we have entered for comparison the average curves for Jacobsen's areas VI (curve B), touching the northern entrances to the Caribbean from (and including) the Anegada Passage east of our profile I to Haiti, and Jacobsen's area XIV (curve A) touching the entire eastern boundary of the Caribbean along the Lesser Antilles to the coast of South America.

From our figure 55 it is now evident that the upper water masses of the Caribbean, above salinity $36.00^0/_{00}$ and a temperature of about 15° C. must be mainly derived from the waters of Jacobsen's area VI (curve B), entering chiefly through the Anegada Passage at the northern end of Lesser Antilles and through the passages between the Greater Antilles.[1] In the deeper layers around the salinity minimum, on the other hand, water masses with characteristics similar to those found North of the Lesser Antilles are the exception rather than the rule, and it is evident that the major portion of the waters of the minimum salinity layer can only have been derived from the water masses of Jacobsen's area XIV (curve A) entering between the Lesser Antilles.

So far our conclusions in regard to the origin of the Caribbean water masses are entirely in accordance with those of Nielsen (1925) who derives the maximum salinity layer from the southern part of the Sargasso Sea to the northeast of the Caribbean and the minimum salinity layer from the southern Atlantic waters to the southeast. But in stating that "Part of the equatorial current, with the subjacent south Atlantic water layer, flows into the Caribbean Sea, but the two are here separated by a stratum with high salinity (over $36{,}5^0/_{00}$) from the Sargasso Sea, which edges in between them at a depth of

[1] If the average curve for the comparatively uniform individual stations of profile II is truly representative in a quantitative sense, waters of the type related to those of Jacobsen's area VI can only represent insignificant admixtures in the minimum salinity layer of the Caribbean.

abt. 200 m.," Nielsen (1925, p. 11), by assuming that the surface water and the intermediate salinity maximum layer are also of different origins (the surface water reverting to the type represented in the salinity minimum layer below), introduces a further complication which at first glance at the temperature-salinity correlation curves alone would appear to be in contradiction of the Atlantis observations of 1933.

In view of the many factors which may cause local or regional variations in temperature-salinity correlation at the very surface, averages for the surface layer as such are obviously more dangerous to use, and less accurately representative than the correlation values determined for deeper strata defined by their hydrographic identity rather than by their bathymetrical occurrence.[1] In our figure 55 the surface layer is therefore only represented by an area towards which both average curves and individual station curves in the Caribbean generally tend to converge, most of them passing through and somewhat beyond to lower salinities at the surface (see figures 58–82), but only very few of them failing to intercept the circle indicated. From the position of this circle relative to curves A and B it would appear that the T-S correlation characteristics of the Caribbean surface and subsurface waters in 1933 were also, like those of the intermediate salinity maximum layer, much more closely related to the corresponding water masses in Jacobsen's area VI (curve B), northeast of the Caribbean, than to those of his area XIV (curve A) to the East and South. It may also be pointed out that when the individual station curves continue beyond the circle marked in the figure, their continuation to lower surface salinity generally follows curve B much more closely than curve A.

But as already above mentioned, the use of the temperature-salinity correlation method for tracing the origin of the surface waters is rather dangerous and much better evidence is actually obtained by a study of the horizontal distribution of surface salinities shown in figures 39 and 40 on pages 54–5. From these figures one will see that

[1] The value of average temperature-salinity correlations for the surface itself is patently limited in full measure by all the objections previously raised (Parr, 1935, pp. 34–41) against the use of T-S correlation points determined by the method of calculating average values of each variate for standard depth, and is further reduced by the disturbing influence of local heating and cooling, evaporation and precipitation, particularly when different layers rise to the surface in a sloping system.

there was not in 1933 a single observation of salinities in the surface layer of the Caribbean region even as low as the surface salinities of Jacobsen's area VI (curve B), not to mention area XIV (curve A), and the prevailing surface salinities in the Caribbean are so much higher than those reported by Jacobsen from area XIV that the difference cannot be explained merely by local external factors. Nevertheless, these figures show that the surface water of lowest salinity occurs exactly in the region of the most rapid inflow from the Southeast, and tend to extend westward along the center of the main surface current as shown by comparison of figure 39 with figures 51 and 53, pp. 71 and 74, while the broad area of higher surface salinities at the northeastern end of the Caribbean, with a northeastern origin indicated by its geographical distribution, is apparently relatively quiescent. Since the same general picture of the location of the main westward flow is also shown in the dynamic topography of the 200 decibar surface relative to the 600 decibar surface, a comparison of the distribution of salinities above 200 meters depth with the dynamic topography based on conditions at deeper levels is valid in this instance. This comparison of horizontal distribution and dynamic topography makes it quite evident that Nielsen's theory of a southeastern origin of the surface water must be in the main correct also for the "Atlantis" observations in 1933, since this relatively fast-flowing southern belt must obviously far outweigh the broad but much more slowly progressing northern surface water in its quantitative importance. It seems reasonable to assume that this surface salinity minimum may represent an extension into the Caribbean of the low salinity central belt of the north equatorial current (see Schott, 1926, pl. VIII) with higher salinities on both sides. Our initial difficulty arose from the fact that the surface salinity observations made by the "Atlantis" in the eastern end of the Caribbean in 1933 agree so very badly with those recorded by Jacobsen from his area XIV immediately outside. This may, of course, in part be due to the lateral as well as vertical mixing to be expected during the passage of the surface water through the narrow straits separating the Lesser Antilles, but the magnitude of the difference is such that it must undoubtedly also to a considerable extent be due to actual differences in the character of the surface water outside of the Caribbean to the East, similar to the fluctuations in this respect within the Central American seas, of which a comparison between figures 39

and 40 (pp. 54–5) showing the "Atlantis" observations in the two successive years 1933 and 1934 give us an excellent example. To attempt to offer an explanation of this change from one year to the next is obviously impossible on the basis of the data now available, so the figures must stand simply as a record of the extent to which the distribution of surface salinities may be subject to fluctuation in this area. It will be noticed, however, that the surface salinities for 1934 (see figure 40) are low enough to be in very good agreement with Jacobsen's data from area XIV, contrary to what we found in the 1933 observations. Under the circumstances it is very unfortunate that we do not know the salinities of the eastern Caribbean also for 1934.

In our conclusions so far, we have thus arrived at a complete confirmation of Nielsen's theory that an intermediate water mass of a northeastern origin injects itself as a salinity maximum layer between a surface layer and a deeper salinity minimum layer entering mainly from the East and Southeast, while the surface water which may enter from the Northeast is relatively unimportant and is left more or less behind in the progression of the main Caribbean current.

On the basis of our conclusions (Parr 1936a, see p. 63) that vertical and horizontal stability must vary in inverse relationship to each other, it is also possible to offer a very simple explanation of this shuffling of North Equatorial and Sargasso Sea waters. Due to the curvature of the Sargassum circulation system, all its water masses must be under the influence of a centrifugal force. Since the maximum salinity layer is generally also a layer of very high velocities, it must be subject to comparatively great centrifugal influence of this sort. At the same time it is also the layer of maximum vertical stability and therefore of minimum frictional resistance to horizontal motion. Its centrifugal force may therefore exert itself more freely, and since it is unopposed by opposite centrifugal forces in the almost rectilinear North Equatorial current, it is unavoidable that the shift outward from the center of the Sargasso circulation should be greatest in the maximum salinity layer.

From these considerations we should further expect the penetration of the maximum salinity layer from the Sargasso Sea into the North Equatorial current and its continuation in the Caribbean, to be strictly limited to the maximum salinity layer alone, that is, it should not exceed the boundaries of the layer of maximum vertical stability,

since it is obvious that the vertically instable layers even immediately above and below could not be involved without overcoming the obstacle of a much greater frictional resistance. That is, the translated layer must move between its own upper and lower boundary sheets, and not against or with involvement of the lower and upper boundary sheets of the vertically instable layers above and below. This would explain the failure of the surface layer to become involved in the translation, and it is also quite in accordance with our finding that the deeper waters already at the 15° isothermal sheet are again of north equatorial origin (see p. 82).

These considerations incidentally suggest a method for approximate determination of the boundaries of the invading wedge. If we have two adjacent water masses of different temperature-salinity correlation characteristics, with a wedge-like lateral extension from one into the other, as shown in the upper portion of our figure 56,[1] it is evident that there must be a thin contact layer in which the characteristics must be exactly intermediate between the features of the original water masses of either side; while the distribution of temperatures, salinity and other characteristics above and below would be dependent upon the rate of exchange through this contact layer. Therefore, if we know the temperature-salinity correlation curves at points A and C (figure 56, top) we may determine approximately the upper and lower limits of the wedge at point B from the intercept of the T-S correlation curve at this point with the median curve between the T-S correlation curves determined for the two original water masses at points A and C. This median curve has been drawn in broken line in the lower part of figure 56, the two solid lines representing a hypothetical case of two distinct water masses and the curve in dots and dash the T-S correlation curve for a cross-section through the wedge at a point corresponding to B in the upper part of our series. Between its intercepts with the median curve at X and Y, the curve B should thus represent water masses belonging to the wedge, while above X and below Y the curve represents original water masses of the type found at point C with such admixture as has occurred through the contact layer. While the writer is fully aware that this method is for

[1] For convenience we assume the isotherms to extend horizontally through both water masses, their differences being thus indicated only in the courses of the isohalines.

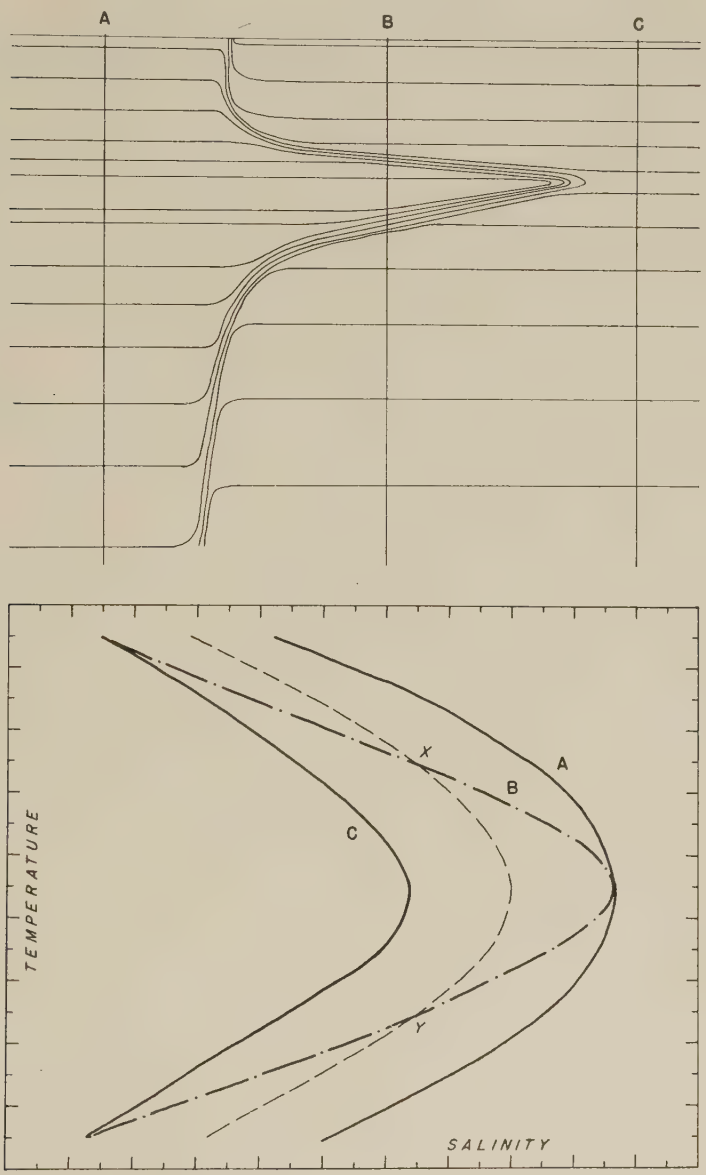

Fig. 56. Temperature-Salinity correlation method for determining boundaries of invading layer. See text.

various reasons[1] only approximate, it is his belief that the approximation will be close enough to be useful when adequate data are available for comparison. The method does, under any circumstance, offer the possibility of a much greater precision in the definition of the wedge than that which can be obtained from a study of salinity and temperature-profiles separately, when both of these characteristics are variable in vertical distribution. The main requirements for applying this method would be an approximate simultaneity of observations and a correspondence of locations transversely to the direction of flow. Unfortunately, neither of these requirements would be fulfilled in an attempt to compare Jacobsen's records from area VI and XIV in the open Atlantic, with our own much later observations at a more advanced point in the current system, and the application of this method to the particular problem in hand must therefore be postponed under further observations become available.

In regard to the fate of the original maximum salinity layer of the North Equatorial current, there are, of course, two possibilities. It may have been shoved farther southward in front of the Sargasso Sea invasion, or it may simply have been split and separated vertically by the advancing wedge of Sargasso Sea water. While the former possibility does not necessitate a change in longitudinal velocity, the latter definitely requires an acceleration of the current to carry off the increased volume. While the dynamic and descriptive hydrographic data are not as yet adequate to show what actually occurs, it is the author's personal opinion that probably most of the original North Equatorial current salinity maximum layer is still present in the Caribbean current and only comparatively little of it has been displaced farther southward.

A further detailed discussion of individual temperature-salinity correlation curves would be rather superfluous, but at one point the author was interested to notice the apparent accuracy with which the temperature-salinity correlation method may be used to trace even the slightest distinctions between overlaying watermasses, identified only by faint undulations in the normally straight portions of the curves. After having observed the closeness with which these minor undulations agreed at stations 1521 and 1522 south of Haiti, the author also entered the curve for the nearest station in the next profile

[1] One reason being our lack of knowledge of the exact level of penetration of the thin edge of the wedge, and of the details of juxtaposition around its boundaries.

(St. 1561) from Jamaica to Haiti, and a good agreement was again obtained, as shown in figure 57. Although no particular conclusions with regard to origins and relationships have been drawn from the

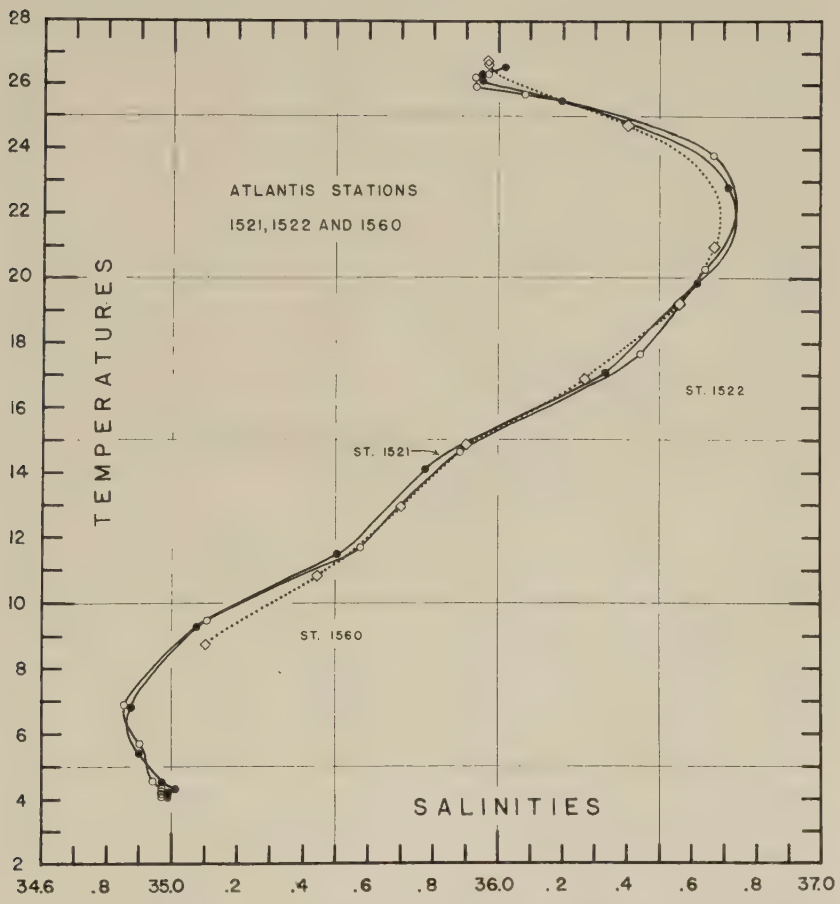

Fig. 57 Temperature-Salinity correlations at stations 1521, 1522, and 1560, illustrating precision of method through consistent agreement of minor undulations in normally straight portions of curves at adjacent stations.

picture in this instance, it furnishes an excellent illustration of the precision with which the temperature salinity correlation method can be applied under favorable circumstances.

SUMMARY AND CONCLUSIONS

The Central American Seas form three distinct basins. Generally accepted designations are available for the Gulf of Mexico basin in the North West and for the Caribbean basin in the South East, but not for the intermediate basin between the Yucatan Channel and the Honduras-Jamaica-Haiti ridge. The name Cayman Sea is proposed for this basin (p. 7).

Vertical profiles of temperatures and salinities are presented for all sections. A general slope from higher levels in the South and West to lower levels in the North and East is pointed out (p. 11). The bathymetric topography of the 15° C. isothermal sheet and the horizontal variations in the thickness of the maximum salinity layer are presented in figures 35 and 36 page 46 and 47. A longitudinal slope to deeper levels in the North West is shown to be superimposed upon the transverse slope of the 15° C. isothermal sheet (p. 45). The thickness of the maximum salinity layer is also found to have a transverse and longitudinal gradient trend, with further superimposition of local variations associated with the general circulation pattern (p. 45).

When corrected for adiabatic effect the bottom waters of the Caribbean and Cayman Seas are found to show a significant decrease in potential temperatures down to the greatest depth (p. 48). Hydrographic data seem to suggest a threshold depth in the Cayman Sea (2500 meters) about 400–500 meters deeper than the threshold depth of the Caribbean (2000–2100 m.), also showing that the bottom waters of these two basins must be entirely separate (p. 52).

The horizontal distributions of surface salinities in 1933 and 1934 show great and incompatible differences in *absolute* values, giving evidence of considerable actual fluctuations in this respect, but agree in the main features of *relative* distributions (p. 53, figures 39 and 40). Relatively low surface salinities seem to develop in the South Cuba Sea (between Cuba and the Cayman ridge) and in a central area south of Jamaica, while relatively high salinities occur in the central portion of the bight between Colombia, Panama and Honduras (p. 56). Both the high and the low surface salinity values seem associated with major eddy movements, but the dangers of using this correlation as evidence of a causal relationship is pointed out (pp. 56 and 77).

The horizontal distributions of maximum and minimum salinities and of salinities in the 15° C. isothermal sheet are presented in figures 41, 42, 44 and 47, pp. 58–66. Certain difficulties in combing the 1933

and 1934 data with reference to the distribution of minimum salinities are pointed out and discussed (p. 57).

The reasons for selecting the 15° C. isothermal sheet, representing the middle of the straight portion of the Temperature-Salinity correlation curves, for an analysis of horizontal distributions in spite of the very slight variations in salinities at this temperature are discussed (p. 60), and the apparent successfulness of the method is pointed out.

It is shown that lateral mixing is apparently much less intensive in the vertically instable 15° C. isothermal sheet than in the vertically stable maximum and minimum salinity layers above and below, and reference is made to the inverse causal relationship between vertical and horizontal stability discussed in a separate publication (p. 63).

Relative dynamic topographies are presented for surface with reference to 200 decibars; 200 decibars with reference to 600 decibars; 600 decibars with reference to 1200 decibars; and for the entire thickness between surface and 1200 decibars (figures 48–51, pp. 68–71). It is shown that by far the greatest current speeds are contained between surface and 200 decibars but that there is no essential change in general circulation pattern in any of the three depth intervals presented separately. The main features of the horizontal circulation are presented in figure 53, p. 74, and it is pointed out that regardless of exact path of flow the main current must ascend a considerable calculated longitudinal dynamic slope to flow from its entries into the Central American seas to its exit through the Yucatan Channel (p. 75).

An automatic mechanism for intermittent renewal of the bottom waters of the Central American basins by inflow along the bottom itself is described (p. 75) and the conclusion is reached that it is the deepest waters in these basins which are of freshest arrival.

The Temperature-Salinity correlation curves are given for all stations (figures 58–82, pp. 93–110). Average T-S correlation curves are shown to give excellent illustrations of progressive mixing between sub- and superjacent water masses (p. 80, figure 55). It is found impossible to combine the 1933 surface salinity observations from the Caribbean with those reported by Jacobsen from Area XIV of the North Equatorial current. Fluctuations in the latter are therefore indicated. Nevertheless the observations are shown to give complete confirmation (pp. 82 and 85) of Nielsen's theory that a maximum salinity layer of Sargasso-sea origin injects itself between the surface layer and the deeper water masses derived from the East and South.

An explanation is offered for this shuffling of water masses and a Temperature-Salinity correlation method is suggested for more precise, although only approximate, determination of the boundaries of an invading layer or wedge under such circumstances (p. 86).

An illustration is given of the great apparent precision of the T-S correlation method under favorable conditions (p. 89, figure 57).

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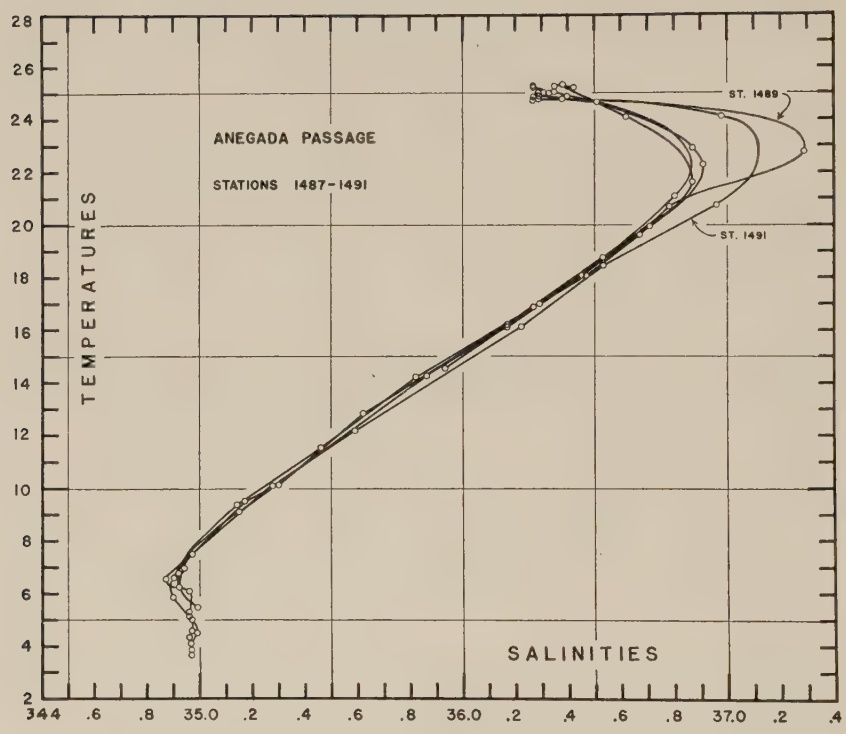
FIGURES 58–82. TEMPERATURE-SALINITY CORRELATIONS IN THE CARIBBEAN AND CAYMAN SEAS. ATLANTIS OBSERVATIONS, 1933 AND 1934.


ANEGADA PASSAGE
STATIONS 1487-1491
ST. 1489
ST. 1491
TEMPERATURES
SALINITIES
28
26
24
22
20
18
16
14
12
10
8
6
4
2
34.4
.6
.8
35.0
.2
.4
.6
.8
36.0
.2
.4
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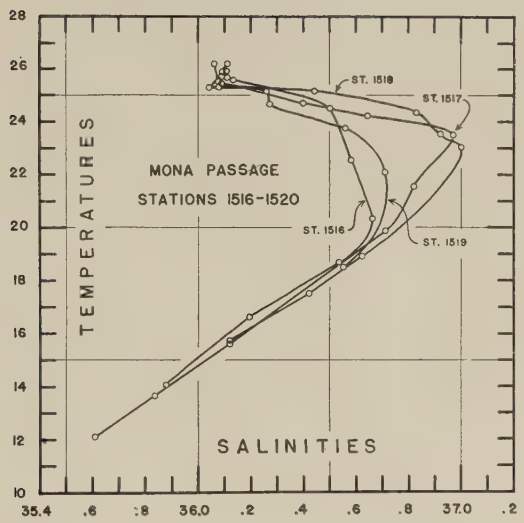
37.0
.2
.4

Fig. 58.


28
26
24
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18
16
14
12
10
TEMPERATURES
MONA PASSAGE
STATIONS 1516-1520
ST. 1518
ST. 1517
ST. 1516
ST. 1519
SALINITIES
35.4
.6
.8
36.0
.2
.4
.6
.8
37.0
.2

Fig. 59.

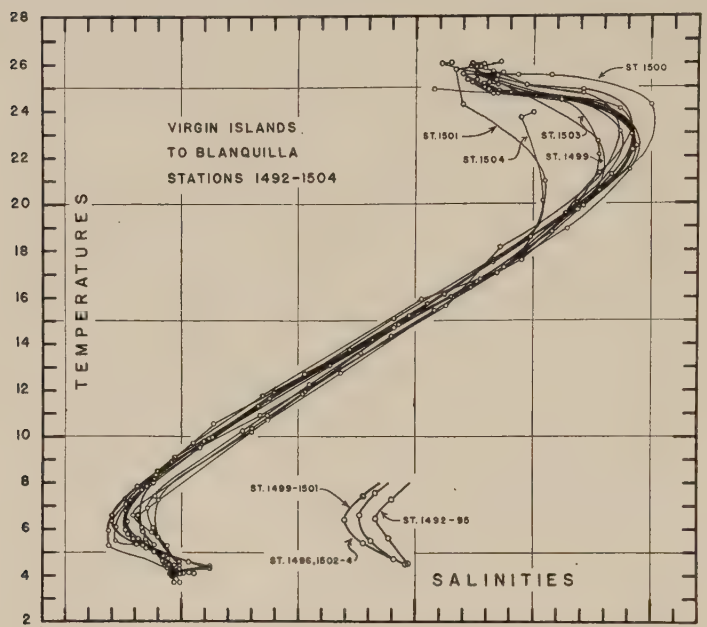

Fig. 60. Stations 1492–1504. With analysis of group averages around minimum salinities.

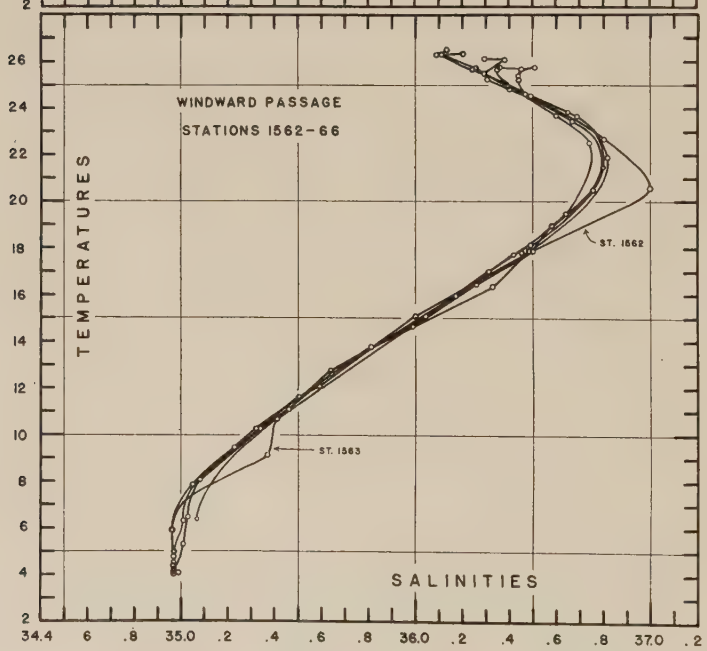

Fig. 61.

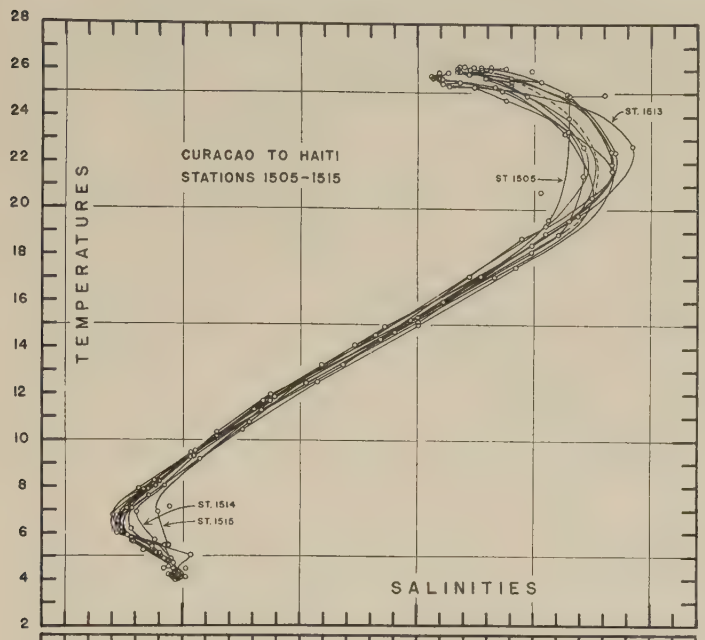

Fig. 62.

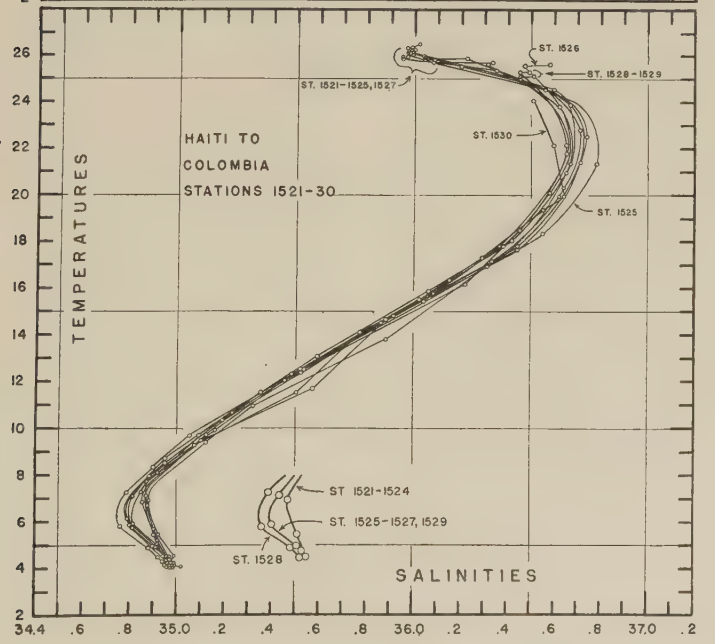

Fig. 63. Stations 1521–1530. With analysis of group averages around minimum salinities.

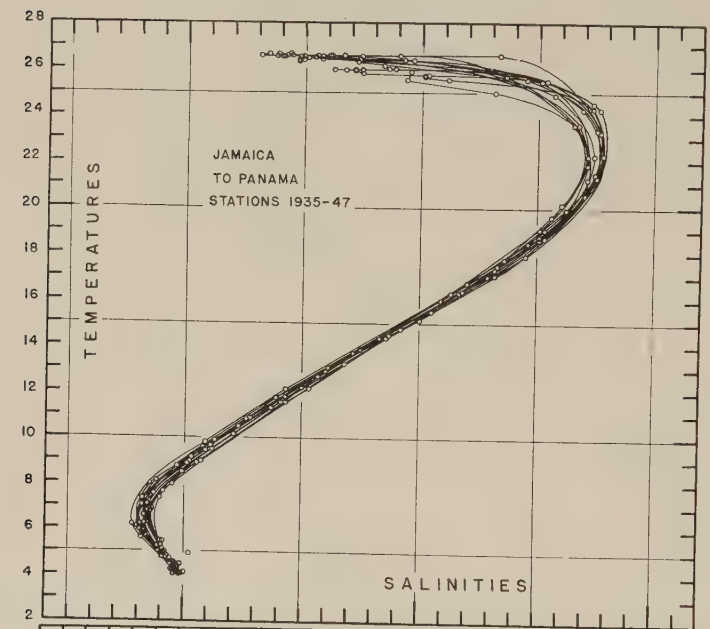
JAMAICA
TO PANAMA
STATIONS 1935-47
TEMPERATURES
SALINITIES
28
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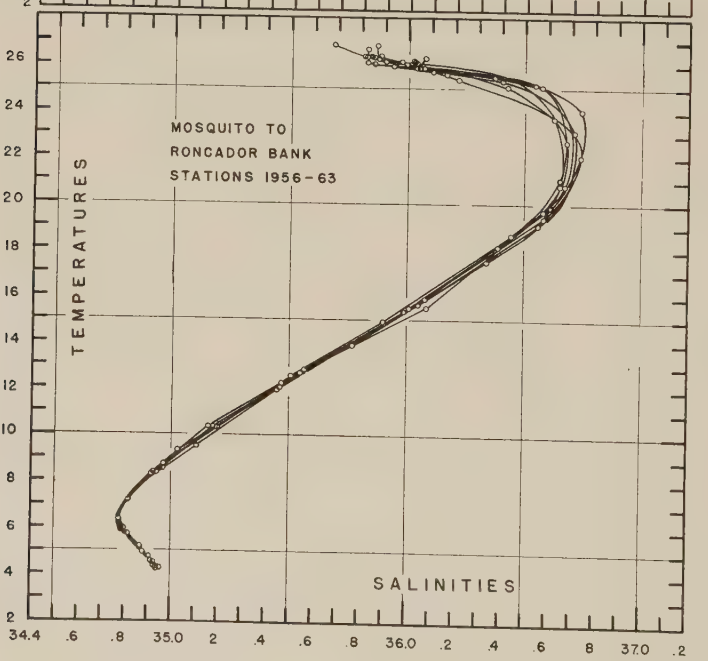
Fig. 64


MOSQUITO TO
RONCADOR BANK
STATIONS 1956-63
TEMPERATURES
SALINITIES
26
24
22
20
18
16
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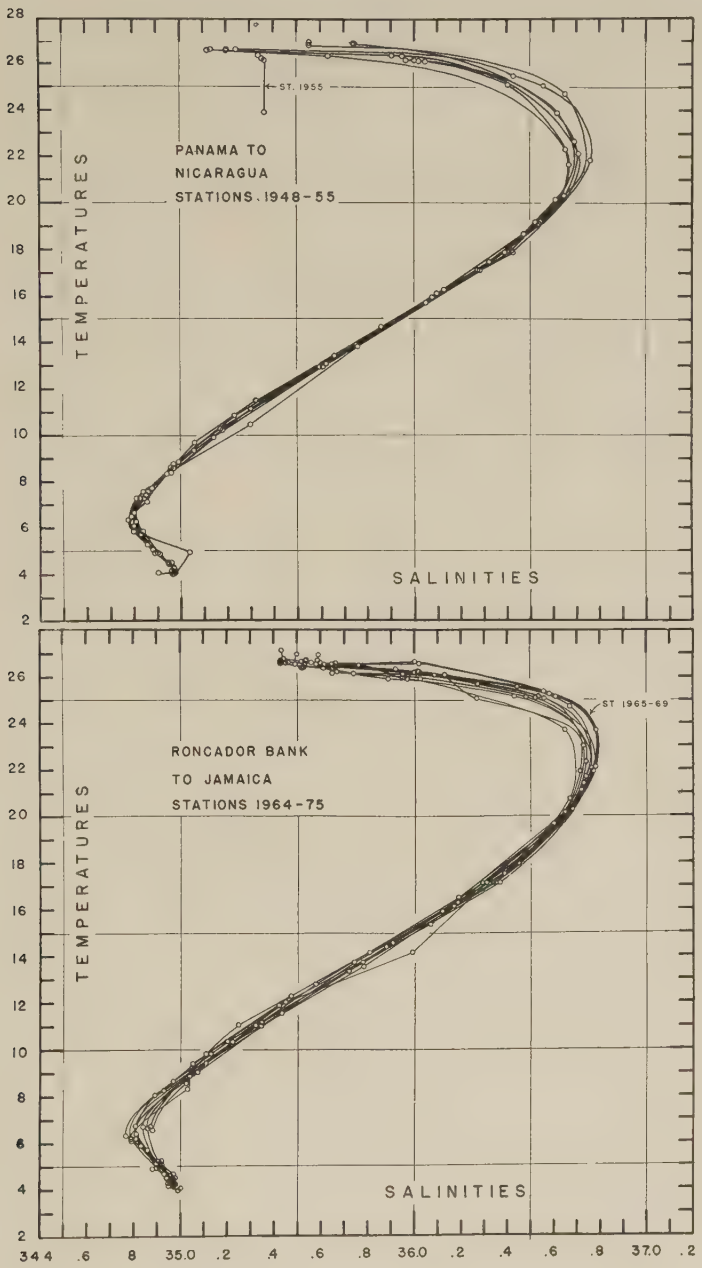
34.4 .6 .8 35.0 2 .4 .6 .8 36.0 .2 .4 .6 8 37.0 .2

Fig. 65.


PANAMA TO
NICARAGUA
STATIONS 1948-55
ST. 1955
TEMPERATURES
SALINITIES
28
26
24
22
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12
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8
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4
2

Fig. 66.

RONCADOR BANK
TO JAMAICA
STATIONS 1964-75
ST 1965-69
TEMPERATURES
SALINITIES
26
24
22
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18
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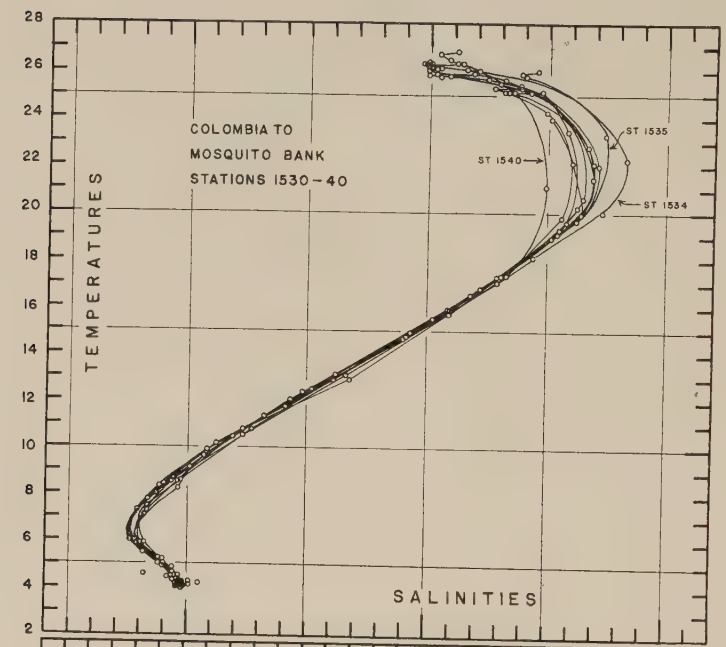
34 4 .6 8 35.0 .2 .4 .6 .8 36.0 .2 .4 .6 .8 37.0 .2

Fig. 67.


COLOMBIA TO
MOSQUITO BANK
STATIONS 1530–40
ST 1535
ST 1540
ST 1534
TEMPERATURES
SALINITIES
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4
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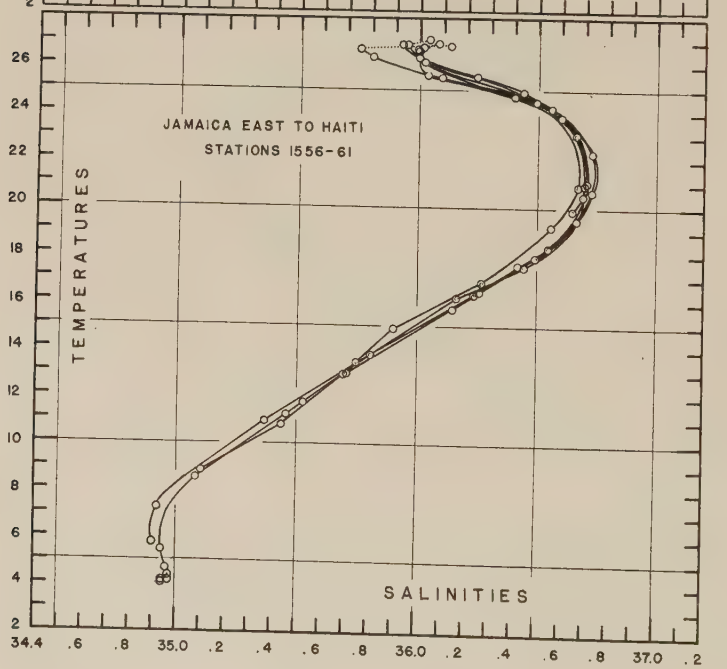
Fig. 68.


JAMAICA EAST TO HAITI
STATIONS 1556–61
TEMPERATURES
SALINITIES
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18
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8
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4
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34.4
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35.0
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36.0
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37.0
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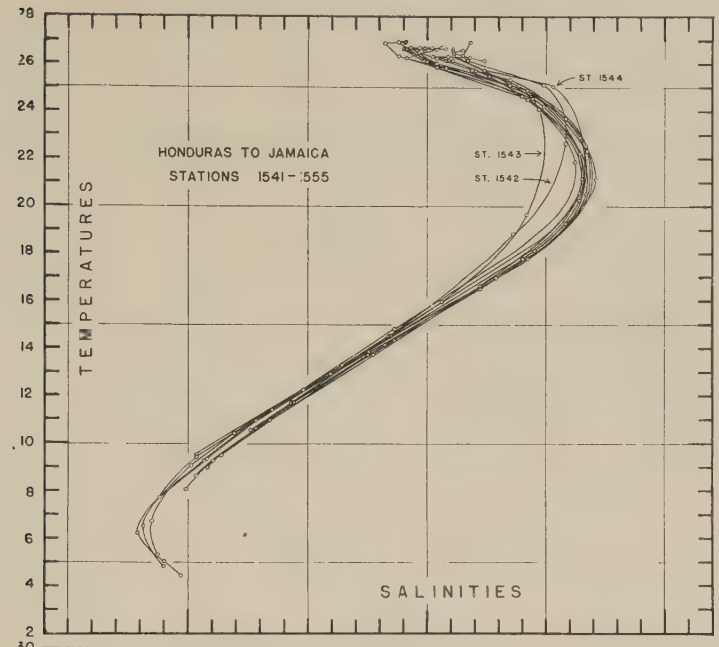
Fig. 69.


HONDURAS TO JAMAICA
STATIONS 1541 - 1555
ST. 1544
ST. 1543
ST. 1542
TEMPERATURES
SALINITIES
28
26
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22
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18
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12
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8
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4
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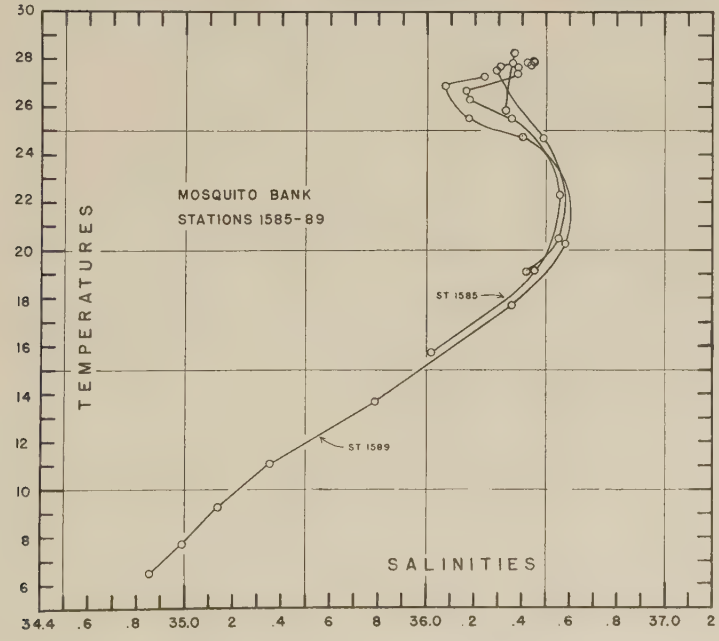
Fig. 70.


MOSQUITO BANK
STATIONS 1585-89
ST 1585
ST 1589
TEMPERATURES
SALINITIES
30
28
26
24
22
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16
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35.0
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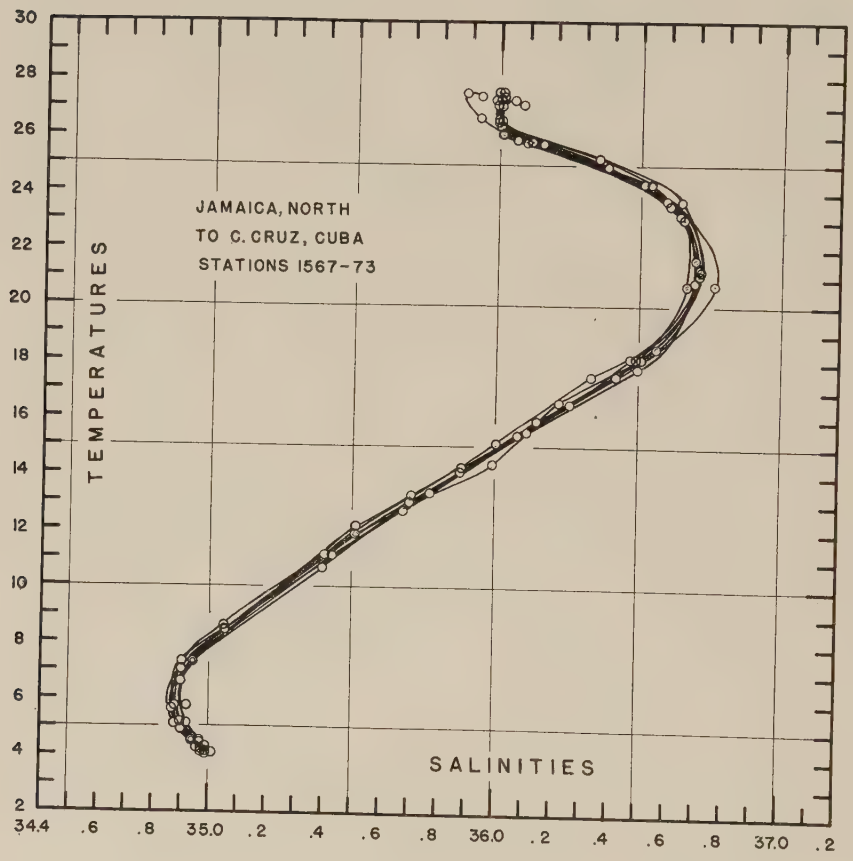
37.0
2

Fig. 71.


JAMAICA, NORTH
TO C. CRUZ, CUBA
STATIONS 1567-73
TEMPERATURES
SALINITIES
30
28
26
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22
20
18
16
14
12
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4
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34.4
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35.0
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36.0
.2
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37.0
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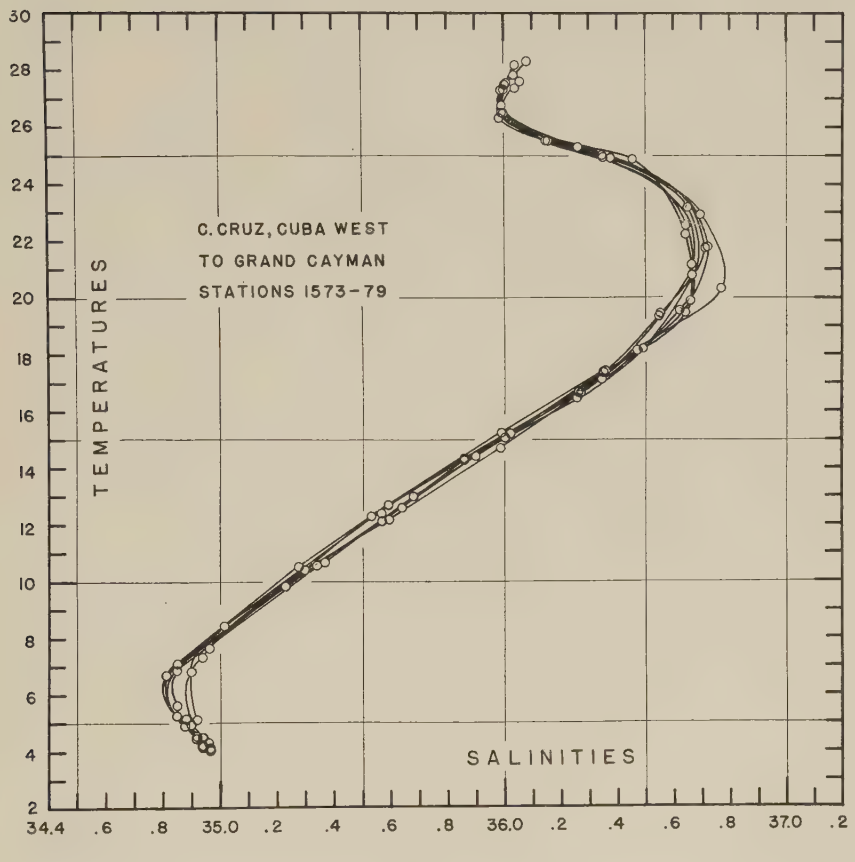
Fig. 72.


C. CRUZ, CUBA WEST
TO GRAND CAYMAN
STATIONS 1573-79
TEMPERATURES
SALINITIES
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34.4 .6 .8 35.0 .2 .4 .6 .8 36.0 .2 .4 .6 .8 37.0 .2

Fig. 73.

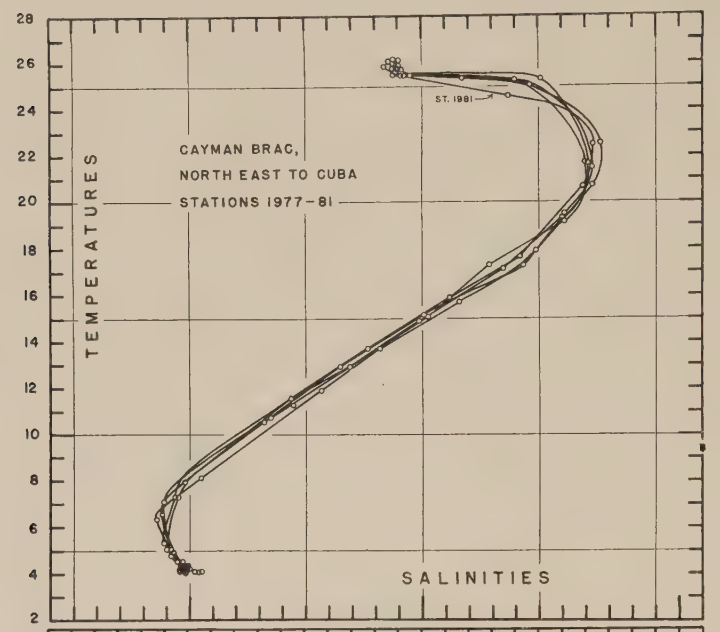

TEMPERATURES
CAYMAN BRAC,
NORTH EAST TO CUBA
STATIONS 1977-81
ST. 1981
SALINITIES

Fig. 74.

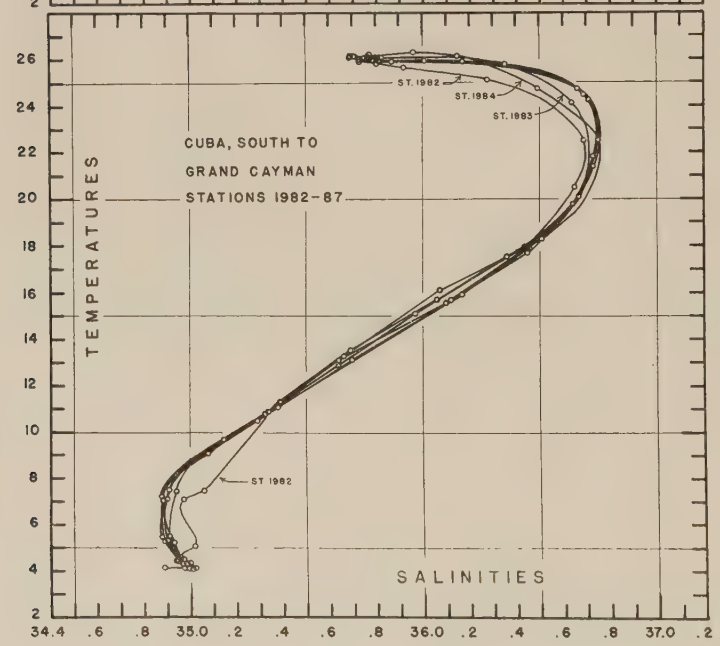
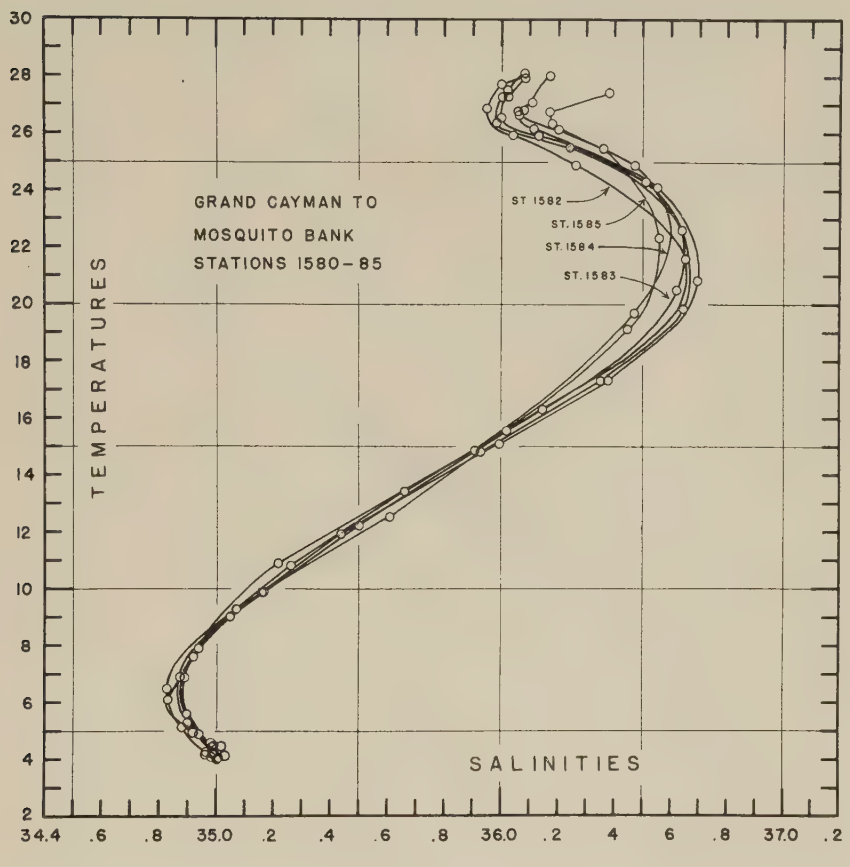

TEMPERATURES
CUBA, SOUTH TO
GRAND CAYMAN
STATIONS 1982-87
ST. 1982
ST. 1984
ST. 1983
ST 1982
SALINITIES
34.4 .6 .8 35.0 .2 .4 .6 .8 36.0 .2 .4 .6 .8 37.0 .2

Fig. 75.


GRAND CAYMAN TO
MOSQUITO BANK
STATIONS 1580–85
ST 1582
ST. 1585
ST. 1584
ST. 1583
TEMPERATURES
SALINITIES
30
28
26
24
22
20
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16
14
12
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34.4
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35.0
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37.0
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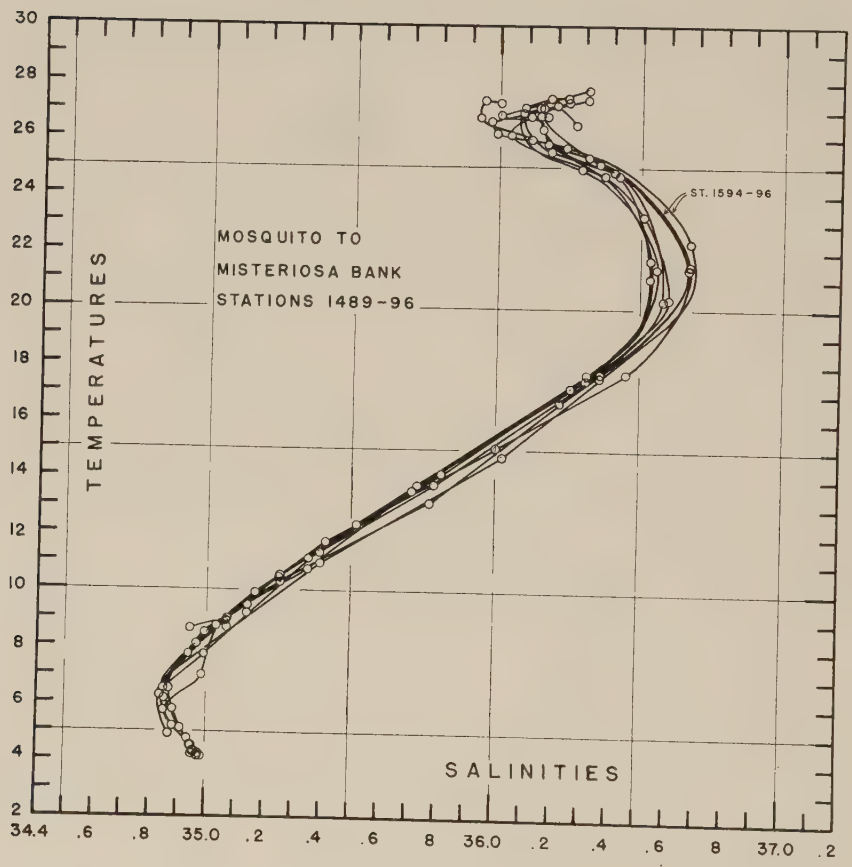
Fig. 76.


30
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2
TEMPERATURES
MOSQUITO TO
MISTERIOSA BANK
STATIONS 1489-96
ST. 1594-96
SALINITIES
34.4
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35.0
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37.0
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Fig. 77.

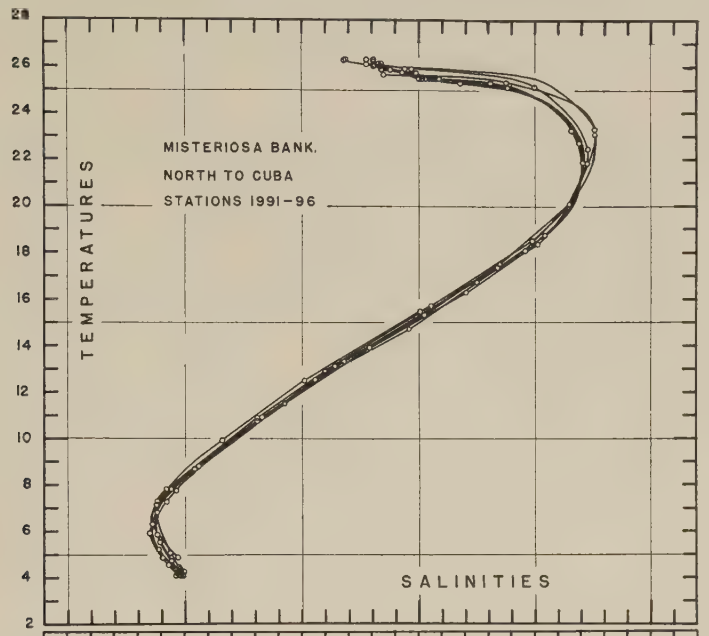
MISTERIOSA BANK,
NORTH TO CUBA
STATIONS 1991–96
TEMPERATURES
SALINITIES

Fig. 78

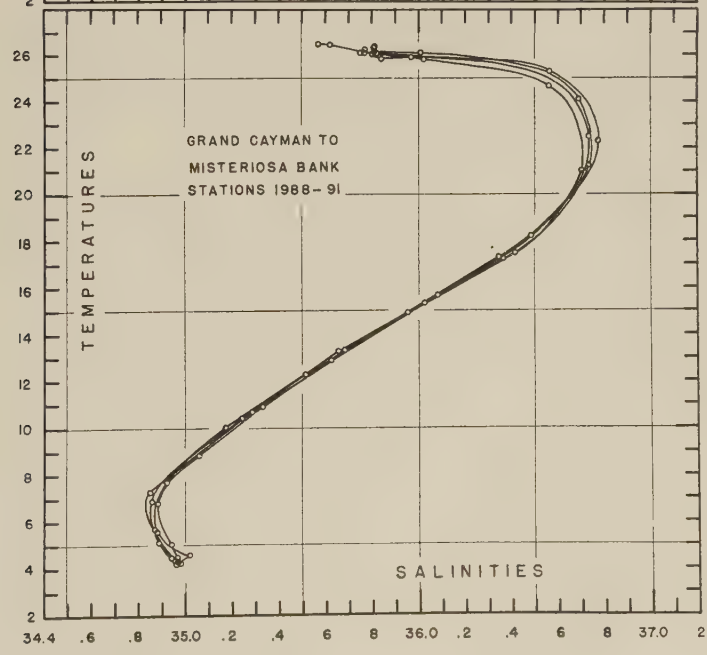
GRAND CAYMAN TO
MISTERIOSA BANK
STATIONS 1988–91
TEMPERATURES
SALINITIES

Fig. 79.

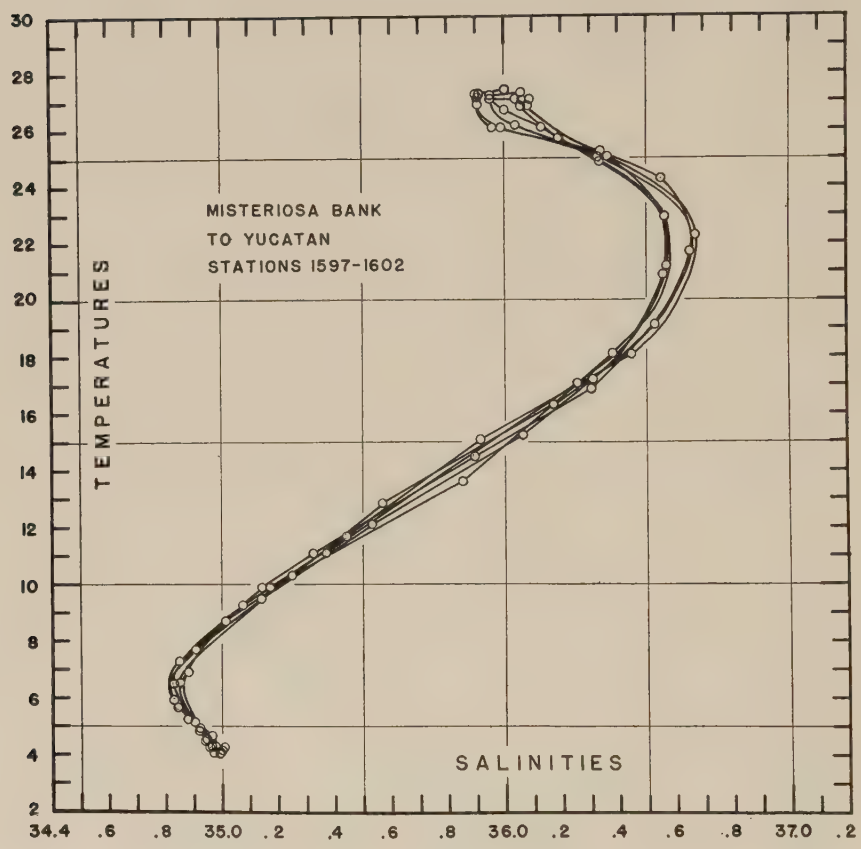
MISTERIOSA BANK
TO YUCATAN
STATIONS 1597-1602
TEMPERATURES
SALINITIES
30
28
26
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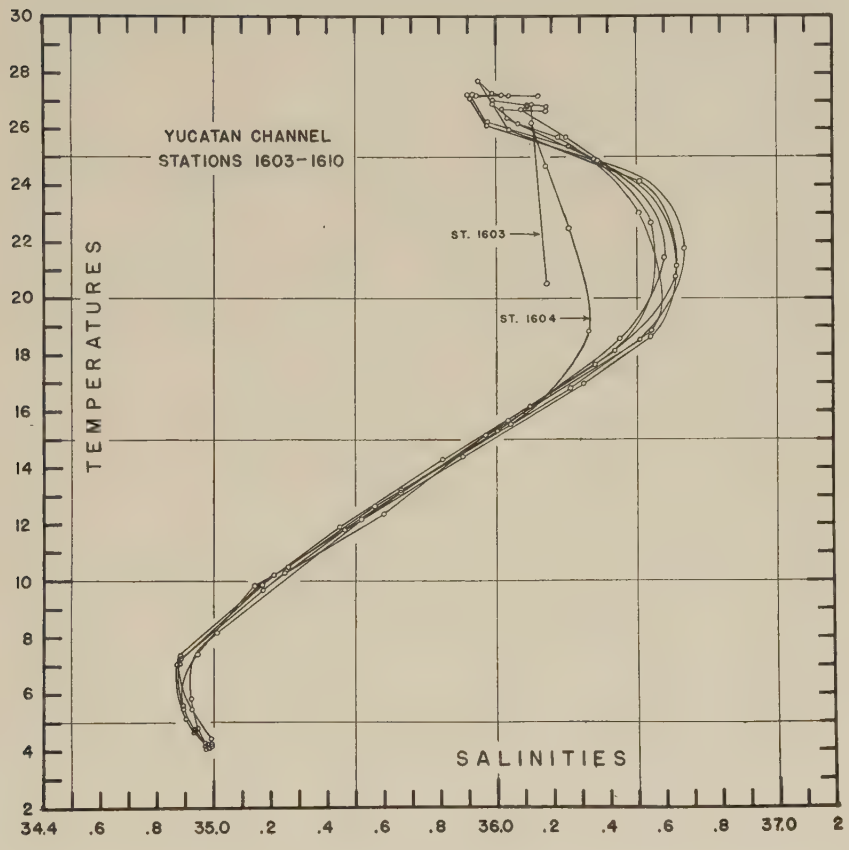
Fig. 80.


YUCATAN CHANNEL
STATIONS 1603–1610
ST. 1603
ST. 1604
TEMPERATURES
SALINITIES
30
28
26
24
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18
16
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12
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6
4
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34.4
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36.0
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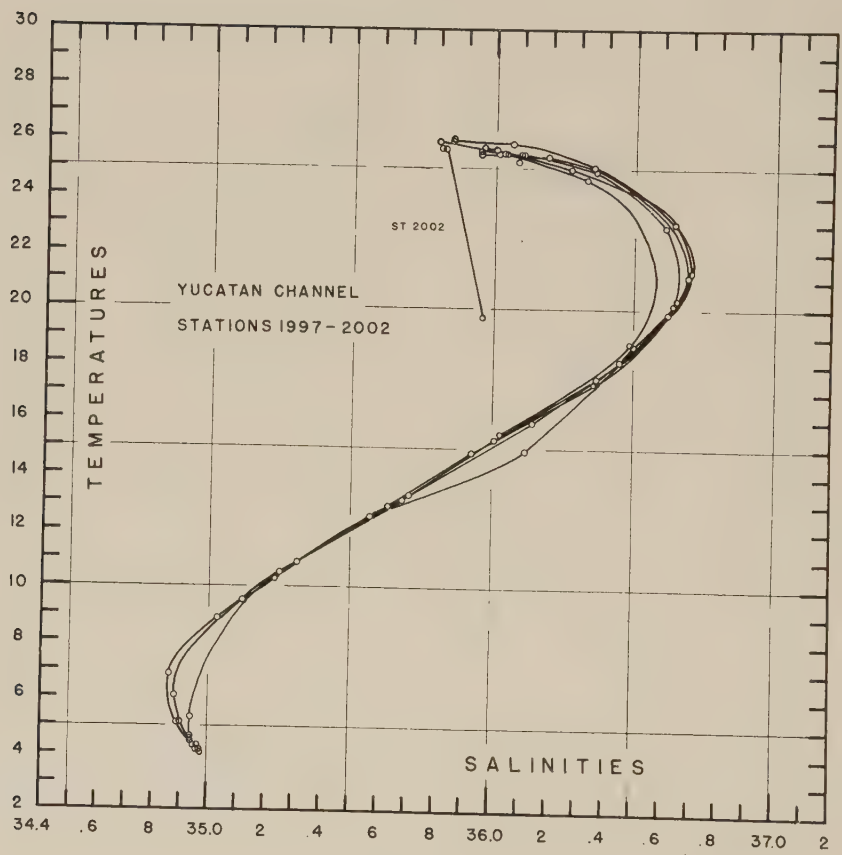
37.0
2

Fig. 81.


30
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TEMPERATURES
YUCATAN CHANNEL
STATIONS 1997-2002
ST 2002
SALINITIES
34.4 .6 8 35.0 2 .4 6 8 36.0 2 .4 .6 .8 37.0 2

Fig. 82.

Contribution No. 126

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EYES OF DEEP SEA CRUSTACEANS

I. Acanthephyridæ

J. H. WELSH AND F. A. CHACE, JR.

(*From the Woods Hole Oceanographic Institution*[1] *and the Biological Laboratories, Harvard University*)

The depths of the ocean impose upon the animals which live there a very different set of environmental conditions from those found at the surface. Absence of sunlight, low temperature, high pressure and viscosity, and a somewhat different chemical composition of the sea water necessitate morphological and physiological modification in the organisms which inhabit deep water. Some of these modifications are well known. For example, if we select the more obvious features which are associated with low light intensity, or even complete absence of sunlight, we must include the presence of photophores, peculiar pigmentation of the body, and adaptation of the eyes for vision at a very low intensity of illumination. The photophores and eyes of certain groups of deep-sea crustaceans and fishes have been studied in some detail in the past and are reasonably familiar to biologists. One of the first and best known studies in which the structure of the eye was related to depth was that of Beddard (1884) on the isopod genus *Serolis*. A similar study was made later (Beddard, 1890) on the genus *Arcturus*. Smith (1886) and Henderson (1888) had already noted the tendency toward degeneration in the eyes of deep-water crustaceans, but neither had made a detailed study of these eyes. Chun's (1896) study of the very unusual eyes of deep-water euphausiids was made from collections of the "Challenger" as were Beddard's.

From the collections of the "Valdivia," Doflein (1904) obtained material for a valuable study of the eyes of deep-sea crabs. Dohrn (1908) described the eyes of a few other crustaceans taken by the "Valdivia." More recently Hanström (1932–33) has had an opportunity to study the eyes of deep-water crustaceans.

The problem which confronted these workers, and many others who have made more casual observations, was to explain why some forms found in deep water have well-developed and apparently functional eyes while others are completely blind or have very degenerate eyes. This still remains the most interesting problem in connection with a con-

[1] Contribution No. 126.

sideration of the effect of depth and hence of diminishing light on the eye. There are many more problems which the older investigators would have doubtless solved if they had had more material from known depths, living material, and a more constant supply.

The regular operation of the research vessel "Atlantis" of the Woods Hole Oceanographic Institution has made it possible to study further the animals of the deep sea and has led to the planning of a program in which the first step has been to investigate more fully the modifications with depth in the eyes of certain of the crustaceans. What happens to the size of the eye, the number of ommatidia, the amounts of reflecting and screening pigments, pigment migration, and the structure of the rhabdomes with increasing depth? What is the relation between the development of the eye and the presence or absence of photophores? Such questions, dealt with in an introductory manner, using for material certain representative deep-sea acanthephyrids or prawns, are those we wish to discuss in the present paper. Final conclusions must await the study of many more types of crustaceans from known depths, but certain tendencies are noticeable in the work thus far carried out.

The authors are indebted to several members of the Woods Hole Oceanographic Institution, particularly to Dr. H. B. Bigelow, and to Mr. B. B. Leavitt from whose collections, made in a study of the vertical distribution of deep-water plankton, some of the material for the present study was obtained. The expense of preparing the eyes histologically has been cared for in part by a grant from the Milton Fund of Harvard University.

Methods

The first problem in understanding the effect of the physical environment on deep-sea animals is to obtain a series of a given species from known levels, sufficiently large so that it is possible to determine the average level at which such a species lives. The use of open nets is unsatisfactory as animals are caught at all levels, and only after a large number of hauls at a given station can an idea of the vertical distribution of a species be determined. Nets which may be sent down to the desired level closed, then opened and towed at that level, and finally closed before being brought to the surface are almost a necessity. To operate two to five such nets, particularly when towing at depths of one to two miles, presents mechanical problems which have been quite adequately solved. The closing net used in deep-water tows from "Atlantis" previous to 1936 is described in a paper by Leavitt (1935). The type

of net used during the 1936 cruise was modified somewhat and was found to be well adapted for collecting material alive or in good condition. It will be described in a later paper.

The locations of stations from which material was obtained in 1933 and 1934 are given by Leavitt (1935). During July, 1935, two stations were made in the Sargasso Sea: Station No. 2462 (42° 29′ N. and 70° 21′ W.) and No. 2463 (42° 27′ N. and 70° 14′ W.). During late August, 1935, one station was made on the inshore side of the Gulf Stream: No. 2475 (38° 25′ N. and 71° 04′ W.). In September, 1936, collections were made at Station 2666 (39° N. and 70° W.) and at Station 2667 (35° 40′ N. and 69° 36′ W.).

Obtaining deep-water animals living and in good condition is a second difficulty. Where there may be a warm surface layer, as on the slope side of the Gulf Stream, the animals coming from deeper layers are subjected to a considerable increase in temperature which, it is believed, is much more damaging than the reduction in pressure. The following temperatures were found in early September, 1936.

	Station 2666 Slope side of Gulf Stream	Station 2667 Sargasso Sea
Depth	Temp. °C.	Temp. °C.
Surface	21.0°	26.2°
200 m.	9.7°	18.3°
400 m.	5.4°	17.8°
800 m.	4.5°	14.9°
1000 m.	4.2°	11.7°
2000 m.	3.6°	4.3°

It may be seen that while there was a difference of 5.2° C. at the surface, at 400 m. there was a difference of 12.4° C. Many more of the larger crustaceans were living when they arrived at the surface at Station 2667 than at Station 2666.

During the two trips in 1935 an opportunity was had for the first time to study living forms. Among the acanthephyrids only one species, *Systellaspis debilis,* was obtained alive in any considerable numbers. The only requirement for keeping this form living was found to be a low temperature. At 10° C. they survived for three days, at the end of which time they were killed; therefore, at that time it was not known how much longer they would have lived. During the 1936 cruise a cooling system was on board which made it possible to maintain tanks of sea water at 5° C. Many more forms were taken alive and several species of crustaceans were kept living for the duration of the cruise. Apparently it is possible to maintain many deep-water forms alive if

they are kept at a temperature relatively the same as that where they normally live.

The material used for histological study was fixed in Bouin's immediately on removal from the nets or, in cases where it was desired to observe pigment migration, was kept illuminated for a period of time before fixing. It was found quite necessary to cut through the carapace in order to obtain sufficiently rapid penetration of the fixative. The paraffin method was used in sectioning the eyes. In estimating relative amounts of pigment it was found desirable to leave some sections of each eye unstained. Ehrlich's hæmatoxylin and a counter of eosin were employed for staining those sections which were used in studying the general structure.

Material

Although certain species of the Acanthephyridæ are so numerous that the possibilities of fishing for these prawns on a commercial scale have been suggested, it was as late as 1881 before more than two species of the family were known. Today, due to the many deep-sea expeditions in the past fifty years, the family is represented by six genera and forty-five species. The acanthephyrids normally inhabit the deeper parts of the sea where the penetration of sunlight is practically immeasurable—the so-called " red prawn-black fish " region.

Like a number of other deep-sea animals which have been known to science for only a short time, the acanthephyrids are a comparatively primitive group. The biramous form of the legs, one of the most distinctive characters of the family, ranks them among the most primitive members of the decapod Crustacea. Their color, with but a few exceptions, is a uniform deep crimson red. In other respects the species may differ so noticeably from each other that a cursory examination would scarcely lead to their inclusion in a single family. The integument varies from a hard, polished, armor-like shell to a membranous skin which is displaced or torn from the slightest handling; the rostrum or " head-spine " is typically long and slender, but in many species it is almost entirely lacking; the legs may be short and comparatively stout, or long, slender and fragile, or they may be modified, as in *Ephyrina,* into broad, lamellate appendages; and the eggs are either so small that many hundreds may be attached to a single female, or so large that twenty-five would be a burden to even the larger species. It will soon be seen that this diversity of form is likewise illustrated by the eyes of these prawns. Since most of the species are strictly bathypelagic or-

ganisms, they probably obtain their food from the detritus that is constantly raining down from the swarms of minute plants and animals at the surface of the sea. They are peculiarly adapted to strain this food from their surroundings; the thoracic legs are all provided with numerous long hairs and spines which apparently form a very efficient, sieve-like basket when the legs are held curved beneath the body. In the genus *Ephyrina* the legs are strikingly wide and flat so that, when held in position, they perform their function in much the same way as the baleen of the whale-bone whales. This modification of the legs for food-gathering is of particular interest when one realizes that the thoracic limbs of most shrimp-like Crustacea are used primarily for walking on the sea-bottom and play no direct part in the swimming movements of the animal. Since many of the acanthephyrids probably spend their entire lives far above the sea-floor, the thoracic legs would be only a hindrance to the progress of the prawn through the water if they were not modified to perform a function entirely apart from that for which they were originally designed.

There are, of course, few barriers to the dispersion of bathypelagic organisms which inhabit a world-wide zone of comparative uniformity of temperature and salinity. Many of the Acanthephyridæ, as in most families containing a like number of forms, are known from a very few specimens and little can be concluded about the distribution of those forms at present; but of the commoner ones, some are practically cosmopolitan, some seem to have a discontinuous range, while still others are confined to a reasonably small area. The Indo-Malayan region has the largest representation of these species, if our present records are reliable, with the North Atlantic second in importance. It is a curious fact that there are at least three reasonably common species in the Indo-Malayan region which so far have not been encountered elsewhere, but all three of these species show a very close relationship to three other forms which have been found almost everywhere except in the Indian Ocean. Much more data must be accumulated before the factors responsible for the specific isolation of bathypelagic organisms are known.

As regards the vertical distribution of the group the available data are likewise incomplete. However, of the forty-five species, thirty have been taken with mid-water nets and must be bathypelagic for at least part of the time. Further investigation will undoubtedly reveal that at least some of the remaining fifteen species seldom go down to the sea-floor. On the other hand, three stout-legged, heavy-bodied forms which have always been taken with the dredge or trawl can safely be termed benthonic animals.

Investigations undertaken in the past few years by Mr. Leavitt on "Atlantis" have yielded invaluable information regarding the actual depths at which we may expect to find acanthephyrids in the North Atlantic. The accompanying tables (Tables I, II, and III) give the depths at which three of the most common Atlantic species have been taken with closing nets. Incomplete as these records are, it is quite evident that *Hymenodora glacialis* normally frequents a deeper zone than either of the other species, a fact which agrees with earlier data. *Acanthe-*

TABLE I

Depths at which specimens of Acanthephyra purpurea have been taken with closing nets by the "Atlantis."

Depth in meters	"Atlantis" Station	Number of specimens	Total specimens
300	1737	1	1
400	2263	10	10
800	2263	65	74
	2462	7	
	2463	2	
920	2216	10	10
1000	2260	1	3
	2263	2	
1400	2263	1	1
1600	2263	1	1
1800	2216	2	2
2200	2263	1	1
2600	2260	2	2

phyra purpurea has been taken in open nets from the surface, where one specimen was collected with a dip-net down to 2800 meters, but the majority have been found between 400 and 1000 meters. *H. glacialis* has been found on two occasions at the surface in the Arctic, and some numbers of that species have been found in the stomachs of arctic seabirds. The shallowest trustworthy record for the species taken with midwater nets, however, is one in which ten specimens were taken in 750 meters, and by far the largest number of specimens have come from

TABLE II

Depths at which specimens of Systellaspis debilis have been taken with closing nets by the "Atlantis."

Depth in meters	"Atlantis" Station	Number of specimens	Total specimens
400	2263	15	15
600	2260	1	1
800	2462	9	9
1800	2263	1	1

depths greater than 1000 meters. This species has also been taken with a closing net by the "Valdivia" Expedition in over 4200 meters in the South Pacific. *Systellaspis debilis* apparently frequents slightly shallower depths than the other two species, regardless of the fact that it is the only one of the three which has not been found at the surface. It has been collected with open nets between 32 and 2000 meters and appears to be most abundant between 150 and 500 meters.

At present little is known of the daily vertical migration of these

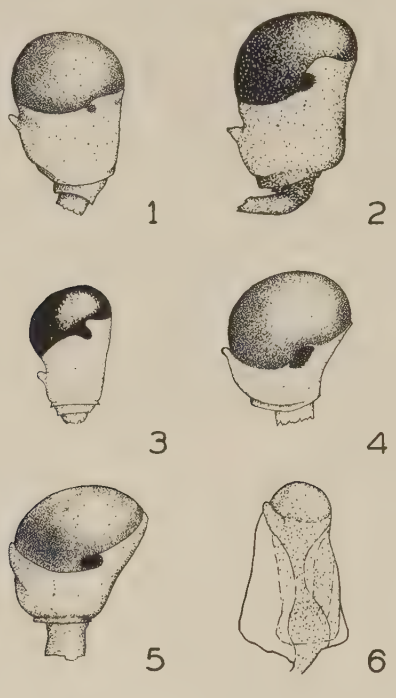
TABLE III

Depths at which specimens of Hymenodora glacialis have been taken with closing nets by the "Atlantis."

Depth in meters	"Atlantis" Station	Number of specimens	Total specimens
1000	2463	2	2
1200	2462	3	3
1400	2263	4	4
1600	2263 2475	2 3	5
2000	1737	3	3
2200	2263	1	1
2600	2260	2	2
2800 to 3200	1739	1	1

species. The results of past expeditions seem to indicate a very slight movement toward the surface at night in *A. purpurea* and *S. debilis* but absolutely none in *H. glacialis* (Murray and Hjort).

An examination of the external features of the eyes of these and other acanthephyrids offers a partial explanation of the above findings. The form of the eyes, although extremely diversified in the group as



(Figures 1–6 are dorsal views of the right eye and eyestalk)

Fig. 1. *Acanthephyra purpurea,* × 5.
Fig. 2. *Ephyrina benedicti,* male, × 4.
Fig. 3. *Notostomus longirostris,* small female, × 5.
Fig. 4. *Systellaspis debilis,* × 7.5.
Fig. 5. *Oplophorus grimaldii,* male, × 7.5.
Fig. 6. *Hymenodora glacialis,* male, × 7.5.

a whole, remains fairly constant within the separate genera. The eyes of the species of *Acanthephyra* (Fig. 1) are of normal size, generally well pigmented with a dark brown pigment and, as in the other genera, the dorsal surface of the eyestalk is provided with an incomplete, deeply pigmented ocellus or accessory cornea, whose function is unknown. In some species the ocellus is complete and entirely distinct from the

true cornea, while in others it may be partially fused with the cornea or even entirely absent. The eyes of *Ephyrina* (Fig. 2) and *Notostomus* (Fig. 3) while similar in size and shape to those of *Acanthephyra* have a jet-black pigment which remains for many years even in alcohol. In *Systellaspis* (Fig. 4) the cornea is considerably larger in proportion to the stalk than in the foregoing genera. The extreme size is attained in the species of *Oplophorus* (Fig. 5) in which the eye may be actually broader than long, and the cornea is generaly set diagonally on the end of the stalk. It is worthy of note that these large-eyed species of *Systellaspis* and *Oplophorus* possibly all possess photophores. The other extreme is found in the eyes of the two species of *Hymenodora* (Fig. 6). In these forms the corneal portion is reduced to a size which is considerably smaller in diameter than the eyestalk. On recalling the records concerning the vertical distribution, it will be seen that those species which have the largest eyes apparently frequent the shallower layers of water, while those with vestigial eyes, like *Hymenodora,* may be termed truly abyssal forms.

The accompanying graph (Fig. 7), despite inaccuracies that can scarcely be eliminated in measuring tissues so subject to alteration after preservation, clearly indicates that the eyes increase in diameter in proportion to the length of the carapace. It is also quite obvious that the degenerate eyes of *Hymenodora* increase in size very little with the growth of the animal. Perhaps the most striking fact brought out by these measurements, however, is that the eyes of *Oplophorus grimaldii* and *Systellaspis debilis,* two forms bearing photophores, are larger in relation to body size than are the eyes of those forms lacking luminescent organs.

Comparative Structure of the Eyes

Fortunately the three most abundant species of acanthephyrids in the North Atlantic and therefore those whose vertical distribution is best known, represent three possible trends in the development of the eye. *Acanthephyra purpurea* is found in greatest numbers within the photic zone, and as it shows a diurnal migration this species must be influenced by the penetrating daylight, although of extremely low intensity. Even in the Sargasso Sea, where the water is very clear, the intensity of blue light at noonday may be reduced to 0.5 per cent of the light at the surface, at a depth of 180 meters (Clarke, 1933). The penetration of other components of daylight into Atlantic waters may be found in a paper by Oster and Clarke (1935). *A. purpurea* is

found far below 180 meters during the day; hence it must be subjected to a very low intensity of illumination.

Systellaspis debilis has much the same vertical distribution as *A. purpurea,* but this form possesses numerous photophores, and, as has already been pointed out, there is an apparent correlation between the size of the eye and the presence or absence of photophores, for species

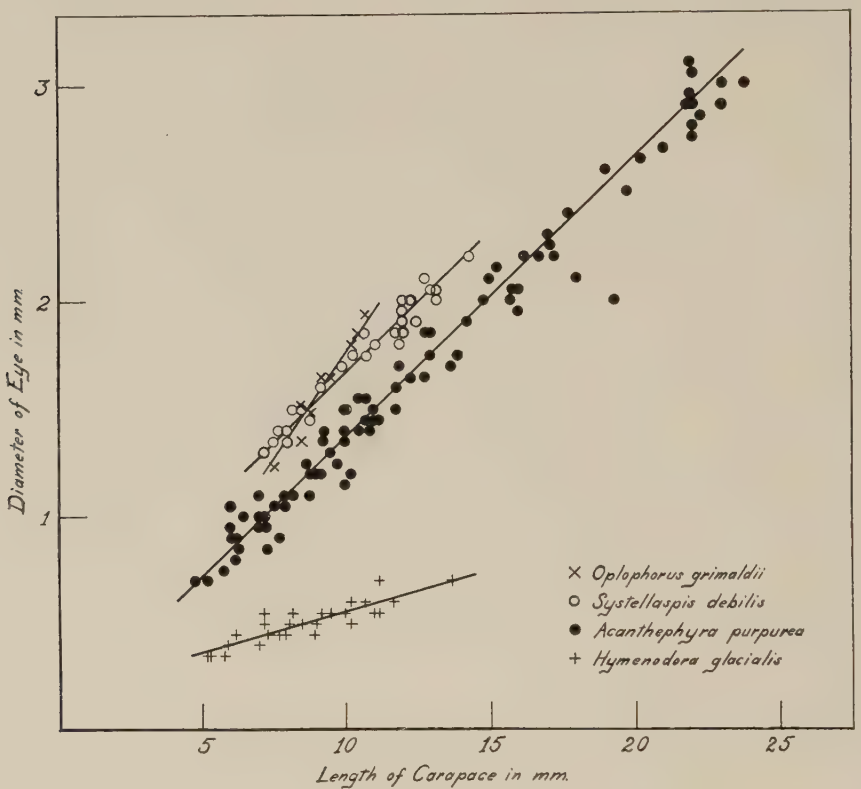


FIG. 7. The diameters of the eyes of four series of acanthephyrids are here shown plotted against carapace length. *Oplophorus* and *Systellaspis* have photophores.

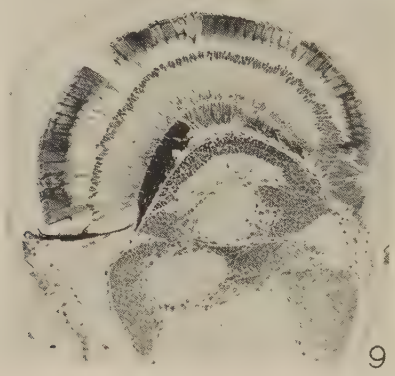
of *Systellaspis* and *Oplophorus* have larger eyes in proportion to body size than the other genera of acanthephyrids which lack photophores.

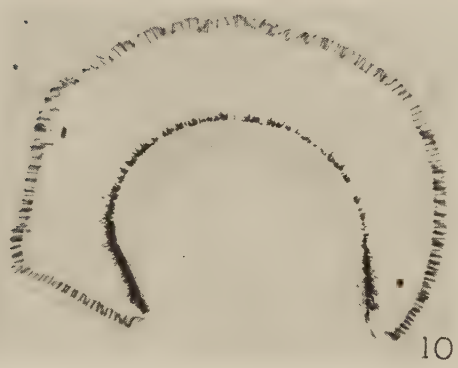
The ability to emit clouds of luminous material is possessed by certain of the deep-sea prawns, as has been mentioned by Alcock (1902) and by Beebe, who observed this phenomenon frequently in his bathysphere descents. So little is known of this interesting method of illuminating the surroundings that it is not possible to hazard a guess as to its effect on the development of the eye.

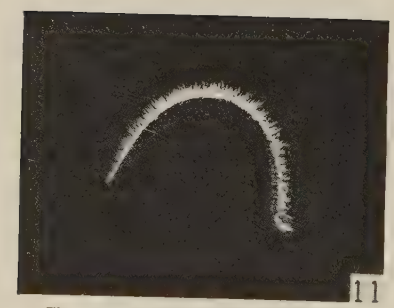
The third species, *Hymenodora glacialis,* inhabits a region well below the photic zone and does not possess photophores and it will be shown that the eyes of this species are very degenerate structurally.

It will not be necessary to describe the general plan of the eye of acanthephyrids for it is basically like that of other decapod crustaceans, and such eyes have been described by Parker (1891), Patten (1887), Trojan (1913), to mention only a few of the earlier investigations of the histology of decapod eyes. From the standpoint of vision and visual acuity the most important features to be considered in any compound eye are the following: (*a*) number of ommatidia, (*b*) development of the rhabdomes (the receptor units), (*c*) amounts, distribution, and movements of screening and reflecting pigments. To these should be added the photosensitive material contained in the rhabdomes. So little is known of the nature of this material that it cannot be discussed at the present time. The average number of ommatidia in a longitudinal section of an eye may be taken as a measure of the total number of ommatidia and thereby the task of counting all the elements is avoided. In all counts the eyes of large, mature individuals were selected, although not the largest obtainable. In eyes of mature *A. purpurea* (Fig. 10) averaging 2.5 mm. in diameter the average number of ommatidia in a section was found to be 145. Eyes of mature *S. debilis* averaging 1.9 mm. in diameter had an average of 81 ommatidia. Eyes of *H. glacialis* averaging 0.6 mm. in diameter had an average of 22 ommatidia. The number of ommatidia, hence the number of rhabdomes, determines in part the visual acuity of an arthropod; therefore the variation in number in these three forms must be significant.

The rhabdomes, whence the fibers of the optic nerve arise, are in a sense the most important structures found in the compound eye. A single rhabdome is formed of parts of the seven functional retinular cells found in each ommatidium, and a longitudinal section presents a peculiar striated appearance. In none of the acanthephyrids which have been studied do the rhabdomes have the well-defined outlines seen in the majority of decapods, including certain deep-water forms. Of the three species being especially considered they are perhaps most definite in *S. debilis,* and may be seen in sections of the eyes of light-adapted specimens (Fig. 15) where they are outlined by the proximal pigment. In *A. purpurea* they are difficult to distinguish (Fig. 9). In all forms taken from the nets during either day or night they were never surrounded by pigment. This means that light entering a given ommatidium could reach the rhabdomes of neighboring ommatidia (Exner, 1891).







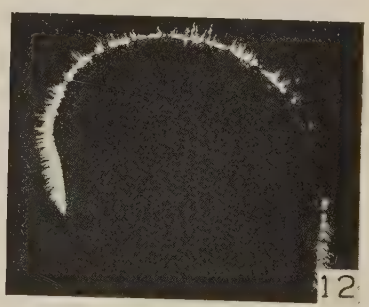


FIG. 8. Dorsal view of the head of *A. purpurea*, × 2.
FIG. 9. Photomicrograph of a section of the eye of a young *A. purpurea*, × 40.
FIG. 10. Photomicrograph of an unstained section of the eye of a mature *A. purpurea*, × 40.
FIG. 11. Reflecting pigment of the eye of a young *A. purpurea* as seen by reflected light, × 35.
FIG. 12. Reflecting pigment of a mature *A. purpurea*, × 35.

In *H. glacialis* the rhabdomes are entirely lacking. The nuclei of the retinular cells remain, and a few nerve fibers leave their vicinity (Fig. 13). At best the eye of this form can be used only as a light receptor. While not as degenerate as the eyes of certain blind crayfish (Parker, 1890) there is certainly not the necessary visual apparatus for image reception.

Eye Pigments

Unpublished results obtained by one of us from keeping certain decapods in constant darkness for a period of months indicate that there may be a gradual reduction in the amount of screening pigment in the eye. This is perhaps to be expected from the work of Odiorne (1933) on the effects of black and white backgrounds on the body pigments of certain fishes. Is there any correlation in the acanthephyrids under consideration between depth and the amounts of screening and reflecting pigment? In practically all decapod crustaceans from shallow water there are two sets of screening pigments. The so-called distal or irispigment is found around the cones, and in many forms such as *Palæmonetes* (Welsh, 1930) it migrates in and out under the influence of hormonal action (Kleinholz, 1936), forming the pseudopupil which helps to regulate the amount of light reaching the rhabdomes. In certain shallow-water prawns which are distinctly nocturnal in their habits such as *Penæopsis goodei* (Welsh, 1935) and species of *Brachycarpus* and *Rhynchocinetes,* the eyes of which have not been described, the distal pigment forms a collar around the outer ends of the cones and remains in that position in light and dark-adapted eyes. In *S. debilis* the distal pigment is present in an amount comparable to that found in nocturnal surface forms while it is slightly less dense in *A. purpurea* and completely lacking in *H. glacialis.* In specimens of *S. debilis,* light-adapted for three hours, there was no measurable migration of the distal pigment. In specimens of both *A. purpurea* and *S. debilis,* fixed directly from the nets either during the day or night, the distal pigment was always in the extreme outer position.

The second set of screening pigment, the proximal pigment, is found in the retinular cells. In dark-adapted eyes of decapods in general, the main mass is found below the basement membrane, while in the light it moves peripherally to surround the rhabdomes and migrates between the plates. In this position it absorbs a large part of the light which reaches the rhabdomes before it has penetrated to any considerable depth. In all specimens of *A. purpurea* and *S. debilis* taken from the nets during the day or night the proximal pigment never surrounded the rhabdomes and the major portion was in the position characteristic

of extreme dark adaptation. In adults of these two species this pigment is present in about equal amounts, but is much less dense than in nocturnal forms found in surface waters. In young of *A. purpurea,* however, the proximal pigment is very heavy in the lateral portion of the eye (Fig. 9). In *H. glacialis* the proximal pigment is entirely lacking as is the distal pigment.

If we assume that the diurnal vertical migrations of *A. purpurea* and *S. debilis* keep these forms in a region of very low but constant light intensity, it would be interesting to know whether the proximal pigment still retains the ability to migrate around the rhabdomes when these forms are subjected to illuminations of high intensity. It was possible to test this point with *S. debilis* and *A. purpurea.* Figure 16 is a photomicrograph of a section of the retina of a specimen of *S. debilis* which had been kept in darkness for three days. Figure 15 is of a similar region of the retina of a specimen kept in diffuse daylight for one hour. During this time the pigment had migrated for some distance peripherally and had surrounded the proximal two-thirds of the rhabdomes. This indicates that the ability of the proximal pigment to migrate still persists even though it may never do so normally in the lifetime of the organism. The proximal pigment of *A. purpurea* is also capable of movement although after prolonged light-adaptation it seldom migrates far into the retinular cells.

The reflecting pigment of decapod eyes is a layer of amorphous guanin which is concentrated around the bases of the retinular cells and acts as a mirror to reflect light back into the rhabdomes (Welsh, 1932). A reflecting or tapetal layer is found in most animals which are active during the night or which live in a region of low light intensity; therefore it is not surprising that this pigment layer is well-developed in the eyes of deep-water decapods.

Explanation of Figs. 13–18

Fig. 13. Section of the eye of *H. glacialis* photographed with transmitted light, × 60.

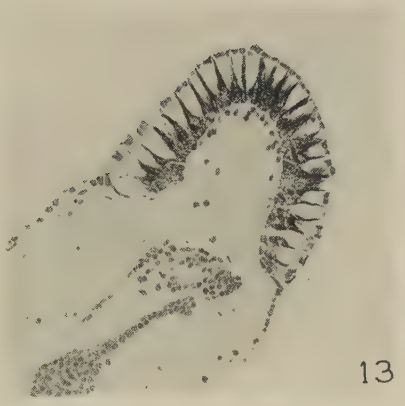
Fig. 14. Section of the eye of *H. glacialis* photographed by means of reflected light, × 60.

Fig. 15. Region of the retinular cells and rhabdomes of a light-adapted eye of *S. debilis,* × 175.

Fig. 16. Region of the retinular cells and rhabdomes of a dark-adapted eye of *S. debilis,* × 175.

Fig. 17. Section of a portion of the eye and the papilla of *O. grimaldii* photographed with transmitted light, × 50.

Fig. 18. The same photographed with reflected light, × 50.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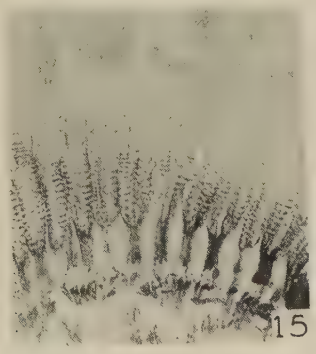
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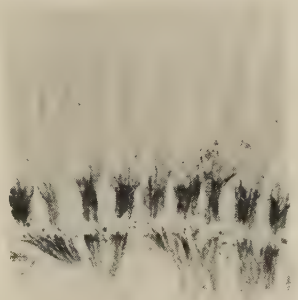
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FIGURES 13–18

The eyes of *A. purpurea* and *S. debilis* have this reflecting layer in addition to the usual screening pigments (Figs. 11 and 12) while *H. glacialis* has only reflecting pigment (Fig. 14). The quantity of reflecting pigment in *H. glacialis* is greater in proportion to the size of the eye than in the other two forms under consideration. It is worth noting that in a series of five species of *Sergestes* which have been studied in a preliminary way there is a rather striking correlation between the amount of reflecting pigment and the depth at which the several forms were taken.

Discussion

The gradual modification of an organ such as the eye as a result of environmental changes, or changes in habit, is one of the fascinating aspects of evolution. A comparison of the eyes of forms which are active at night with those which are active during the day reveals structural and functional adaptations which are among the best examples of the manner in which living material may be modified by external conditions. The degeneration of the eye of cave crayfishes (Packard, 1888; Parker, 1890) is a striking illustration of the disappearance of a useless organ. In the sea we have a gradual reduction in the amount of sunlight which penetrates into the water until a depth is reached, which varies with the locality, at which there is a complete absence of sunlight. The animals of the deep sea have without much question evolved from shallow water forms. Their eyes have become modified depending on the depth to which they have migrated. In regions of low light intensity they are, in general, so changed by an increase in size, loss of screening pigment, and in other ways that they are doubtless quite effective organs of sight. Below the level to which light penetrates some are degenerate and some are completely lacking. On the other hand, some are large and, structurally at least, well adapted for vision or for light reception. This fact still remains as one of the most baffling problems associated with the biology of deep-sea animals. Can there be enough light produced by luminescence to account for the well-developed eyes of some abyssal forms, particularly those living on bottom? This is the question with which most discussions of the eyes of deep-sea animals have ended. It is our hope that if the opportunity remains to continue these studies this question may be satisfactorily answered.

Summary

1. Three species of acanthephyrids have been taken in closing nets in the region of the Sargasso Sea and in slope water near the Gulf

Stream in numbers sufficient so that their vertical distribution is quite accurately known.

Acanthephyra purpurea and *Systellaspis debilis* are found mostly within the photic zone. *Hymenodora glacialis* inhabits a region below that to which sunlight penetrates.

2. The eyes of *A. purpurea* and *S. debilis* are quite similar structurally to the eyes of shallow-water prawns, except that there is less screening pigment.

3. Species of *Systellaspis* and *Oplophorus* possess photophores and the eyes of these forms are larger in proportion to body size than the eyes of those acanthephyrids which lack photophores.

4. The eyes of *H. glacialis* are quite degenerate. The rhabdomes, and both distal and proximal pigments are lacking. The reflecting pigment layer is well developed.

5. Characteristic movements of the proximal pigment of *S. debilis* and *A. purpurea* occur as the result of light adaptation.

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THE CYCLE OF ORGANIC PHOSPHORUS IN THE GULF OF MAINE

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It is generally recognized that the fertility of the sea depends upon a cycle in which carbon, nitrogen, phosphorus and other substances are assimilated under the influence of photosynthetic processes in surface waters and are set free again by processes of digestion or decay. The total organic productivity of a region is limited to the rate at which this cycle is completed. While it is apparent that in many localities the principal limiting factor is the rate of restoration of the inorganic products of decay (NO_3, PO_4) to the surface or photosynthetic zone, little is known concerning the exact locus within the sea at which decomposition actually sets these substances free, or of the rate at which the cycle as a whole or in part is completed.

The concentration of the ultimate products of decomposition, such as NO_3 and PO_4, tell us little about these points since they are stable substances capable of accumulating over a long period of time to high concentrations, and of being transported far from their place of origin. The actual site of decomposition is better indicated by the presence of intermediate products of decay such as ammonia, nitrite, and organic compounds of nitrogen and phosphorus.

The present paper is an account of the distribution of phosphorus throughout the year at a standard station in the Gulf of Maine. At all depths the amount of phosphorus present has been measured in three forms: (1) inorganic phosphate (PO_4), (2) dissolved organic phosphorus, and (3) particulate organic phosphorus. The analysis of these data gives some indication of the magnitude of the synthetic and disintegrative processes undergone by phosphorus compounds in different parts of the water column at different times of year, and of the extent to which phosphorus is transported from one depth to another.

The station chosen for study was located in the deeper portion of the western basin of the Gulf of Maine, 30 miles northeast of Highland Light. The surface water in this region is apparently relatively free from strong non-tidal currents, being sufficiently far offshore to avoid the coastal drift which accompanies the freshening of the water along

[1] Contribution No. 127.

the margin of the Gulf. In this part of the Gulf, as the result of freedom from strong currents, there develops each summer maximal surface temperatures and maximal stability of the water column. In this location one also finds relatively deep water (230–270 meters) free from strong non-tidal currents. Preliminary measurements made by Dr. E. E. Watson with current-meter indicate maximal tidal velocities of 11 cm. per second at 40 cm. above the bottom, and 14 cm. per second at 177 cm. above the bottom. The oxygen content in the deep water below 200 meters is low, varying from 4 to 4.5 cc. per liter. The point chosen for study thus presents conditions in which there exists above the bottom a considerable column of water too poorly illuminated to permit of photosynthesis, which terminates at a depth of 40 to 50 meters (Clarke and Oster, 1934) and in which decomposition occurs in sufficient magnitude to maintain a low oxygen concentration, and one

TABLE I

Station positions and dates.

Atlantis Station Number	Date	Location	Depth of water
			meters
2440	May 18, 1935	42° 22′ N. 69° 35′ W	249
2468	August 20, 1935	42° 20′ N. 69° 32′ W	232
2493	November 8–9, 1935	42° 21.5′ N. 69° 32′ W	256
2495	February 26, 1936	42° 22′ N. 69° 33′ W	270
2558	May 14, 1936	42° 27′ N. 69° 31.5′ W	254

as well chosen as may be to avoid disturbances due to the non-tidal drift of the water.

Stations were made on five occasions separated by intervals of three months, thus completing one yearly cycle. Their positions and dates are given in Table I. The approximate position is indicated by a circle in Fig. 1.

ANALYTICAL PROCEDURE

Inorganic Phosphate

Phosphate samples were collected in black bottles and analyzed for inorganic phosphate at room temperature on shipboard by the Deniges-Atkins method, except that the solution of stannous chloride used contained 0.1 gram $SnCl_2.2H_2O$ in 10 ml. of 1 to 10 hydrochloric acid. Salt effect correction factor as measured was 1.35. Corrections for salt error and reagent blank were both applied.

Particulate Organic Phosphorus

Samples of water of about 300 ml. volume were filtered on shipboard as soon after collection as possible.

The procedure by which particulate organic phosphorus was determined is as follows. The particulate matter is filtered out by suction on a precipitate of barium sulfate on a 3G4 Jena sintered glass funnel with polished surface. The barium sulfate precipitate is

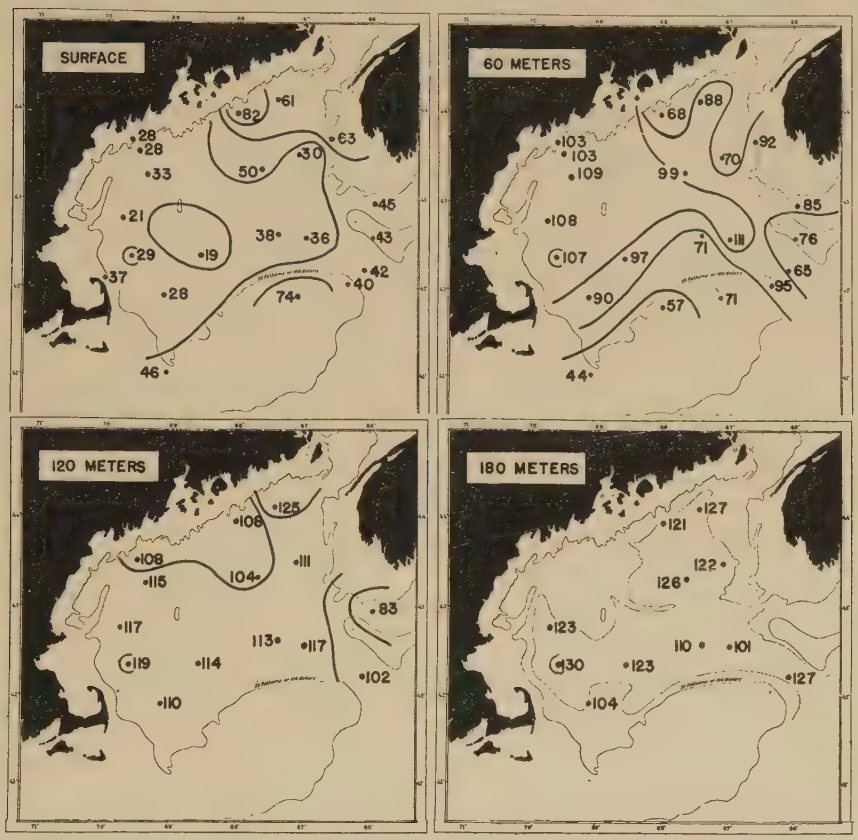

FIG. 1. The distribution of inorganic phosphate, PO_4, throughout the Gulf of Maine in May, 1934, at the surface and at the depths of 60, 120, 180 meters. The circle indicates the position of the stations at which the present investigations were made.

prepared by stirring 0.6 ml. of normal barium chloride into about 10 ml. of hot water containing excess sulfuric acid. It is poured over the funnel, the liquid sucked through, and filter and flask washed thoroughly with distilled water. The sea water sample is run through the

filter, and the volume of the filtrate measured. Plankton and barium sulfate are washed off the filter into a 125-ml. Erlenmeyer flask with a stream of distilled water. The sides and bottom of the filter are cleaned with a rubber policeman and all the precipitate transferred to the flask to insure removal of the plankton. The funnel is cleaned by reverse suction, treatment with sulfuric and chromic acids and thorough washing.

After the addition of 2 ml. of 38 per cent (by volume) sulfuric acid to the plankton, the flask is evaporated on the steam-bath to charring of the organic matter. The flask is ignited to fumes of sulfuric anhydride, and a drop of phosphate-free hydrogen peroxide (Cooper, 1934) (prepared by vacuum distillation of concentrated hydrogen peroxide) is added. A few seconds heating without loss of sulfuric anhydride fumes suffices to destroy the organic matter. The excess hydrogen peroxide is decomposed by heating the sample at 120° C. for one hour on an oil-bath. The cooled samples are diluted with ca. 50 ml. of distilled water and warmed on a steam-bath before filtering through a sintered glass funnel to remove the barium sulfate. The filtrate is diluted to 100 ml. in a glass-stoppered bottle. After the addition of 2 ml. of $2\frac{1}{2}$ per cent ammonium molybdate each sample is shaken. Standards of similar phosphate content as potassium dihydrogen phosphate are made up with 2 ml. of 38 per cent sulfuric acid, 2 ml. ammonium molybdate and distilled water to 102 ml. and shaken. Two drops of stannous chloride solution containing 2.5 grams $SnCl_2.2H_2O$ in 100 ml. of 1 to 10 hydrochloric acid are added to each sample and standard with immediate shaking. After five minutes the samples are compared with the standards in a colorimeter with about 30 cm. depth of solution. Phosphate in the reagents for the development of the color (designated as Blank A) is determined by intercomparison of dilute standards. Phosphate introduced in the treatment of the unknowns (designated as Blank B) is determined by carrying through the procedure on a barium sulfate precipitate not treated with sea water. Blank A is added to the standards to give their true phosphate content. Both Blanks A and B are subtracted from the phosphate found in the unknowns. The net phosphorus in grams $\times 10^{-6}$ found in the unknowns multiplied by $\frac{1{,}000}{\text{ml. sample}}$ gives the plankton phosphorus in grams $\times 10^{-6}$ per liter. Errors in the analysis due to loss of phosphorus by volatilization or change in acidity by loss of sulfuric anhydride are shown to be negligible by carrying through blank analyses with known amounts of added phosphorus.

A procedure employing nitric acid as the oxidizing agent (Robinson

and Kemmerer, 1930), in which the nitric acid was evaporated off and the last traces removed by an evaporation with hydrochloric acid gave check results with the hydrogen peroxide procedure but a poor color match with the distilled water standards. It might be possible to use a procedure similar to that of von Brand (1935) for separation of the diatoms from sea water. No effort was made to differentiate between phosphorus and arsenic in the plankton phosphorus determinations. It was found, however, that the procedure of Zinzidze (1935) using bisulfate and sulfuric acid will bring about the complete reduction of at least 9×10^{-6} grams of arsenic to the limit detectable by the cerulio-molybdate method (2×10^{-7} grams) and make possible a distinction between phosphate and arsenic in plankton analyses.

Dissolved Organic Phosphorus

The phosphorus in solution in organic combination was obtained by subtracting the inorganic phosphorus from the total phosphorus in the filtrate from which the particulate matter had been separated. The following procedure for the determination of total phosphorus in a sea water sample was devised with a view to avoiding the interference of pentavalent arsenic with the ceruleo-molybdate phosphorus determination and to insure the complete destruction of organic matter. In the more rapid methods of analysis which have been used, in which sea water is treated directly with oxidizing agents, arsenic in the sample is oxidized and not subsequently reduced, while organic matter is not completely destroyed in solutions containing large amounts of chloride.

Fifty-milliliter samples of sea water are treated with 3 ml. of concentrated sulfuric acid (arsenic-free) in a 125-ml. Erlenmeyer flask. After evaporation on a steam-bath under a hood to carbonization of the organic matter, each sample is evaporated to the formation of fumes of sulfuric anhydride with swirling to avoid bumping. A drop of phosphorus-free 5 per cent hydrogen peroxide (prepared by vacuum distillation of 30 per cent hydrogen peroxide) is added. The flask is heated in the same manner without loss of sulfuric anhydride for half a minute more to make the solution colorless. If necessary, more hydrogen peroxide may be added. About 60 ml. of distilled water is added to the cooled sample, which is set on the steam-bath for complete solution of the precipitated salts. After transfer to a 500-ml. Erlenmeyer and addition of 8.5 ml. of concentrated ammonia water, the excess of ammonia is boiled off and the volume of solution reduced to about 30 ml. The sample is transferred to a small ground-glass-stoppered bottle and warmed on the steam-bath, open, with 2.47 ml. of 38 per cent (by volume) sulfuric acid. Four milliliters of 10 per cent

sodium sulfite (anhydrous, or hydrated salt in double the concentration) is added, and the stopper held in with a clip to prevent the escape of sulfur dioxide. Excess hydrogen peroxide is immediately destroyed, but eight hours heating on the steam-bath is necessary to reduce pentavalent arsenic to the trivalent form. The sample is transferred to a 500-ml. Erlenmeyer, boiled for five minutes to remove sulfur dioxide, cooled, and diluted to 100 ml. in a ground-glass-stoppered bottle. The residual acid in the sample is 2 ml. of 38 per cent sulfuric. After the addition of 2 ml. of 2.5 per cent ammonium molybdate the sample is shaken. Standards which will develop about the same color intensity as the unknowns are made up from a potassium dihydrogen phosphate solution with the addition of 2 ml. 38 per cent sulfuric acid, 2 ml. of 2.5 per cent ammonium molybdate solution, and distilled water to 102 ml. These are shaken. Each standard and sample is again immediately shaken after the addition of two drops of a solution containing 2.5 grams of $SnCl_2$ $0.2H_2O$ in 100 ml. of 1 to 10 hydrochloric acid. After four or five minutes for the development of the color the samples are compared with the standards in a colorimeter with about 30 cm. depth of solution.

Intercomparison of dilute standards in distilled water is made to estimate the phosphate in the reagents for producing the color (designated Blank A). A blank determination carried through with reagents alone gives the phosphate introduced by reagents in the treatment of the sample (designated Blank B). Blank A is added to the standards to give their true strength in calculating the phosphate in the unknowns. Both Blanks A and B are subtracted from the phosphate found in the unknown. The salt effect correction has been determined as 0.885 for unknowns by analysis of the same sea water with varying amounts of phosphate added. The slope of the graph of phosphate added against phosphate recovered is the salt effect correction. No variation in salt effect correction was found with salinity from 31.5 to 38.5. A similar procedure gave a salt effect correction of 0.81 in determining Blank B. Change of salt effect correction with temperature was not studied but extremes of temperature were avoided in making the analyses.

Since several samples of sea water gave identical analyses with or without the addition of as much as 165 mg. per cubic meter of arsenic (about eight times the amount found in sea water), arsenic was assumed to be reduced completely by the procedure used. Reduction of arsenic in solutions for determining Blank B was found to be much slower than in sea water samples and quantitative only for amounts of added arsenic equivalent to 50 mg. per cubic meter or less. The

difficulty was avoided by the use of reagents containing negligible amounts of arsenic. Schering-Kahlbaum "pro analysi" sulfuric acid was found suitable. The method can easily be adapted to use with a photometer although this was not attempted.

Table II, containing representative data from the analysis of samples of sea water, illustrates the procedure used in computing the dissolved organic phosphate, and gives some indication of the dependability of the methods. The total phosphorus in the samples obtained by combining the phosphorus in the filtrate with the particulate phosphorus retained by the filter (column IV) is compared with the total phosphorus in the water obtained by direct analysis without filtration (column V). It is evident that some small losses result from filtration, but these do not greatly exceed the normal variation of the Deniges-Atkins method. The values for the particulate phosphorus are small, but are consistent within themselves. The smaller values do not greatly exceed that of the blanks employed and in one set of data (for Station 2468, August 20, 1935) the values for the particulate phosphorus are in doubt owing to uncertainty in the value of the blank. The values for dissolved organic phosphorus in these samples are consistently positive and larger than the apparent errors of the method. During a large part of the year, as will be shown, much less soluble organic phosphorus is present in the water. Since this fraction is obtained by taking the difference of two large measures, each subject to considerable errors, it sometimes eventuated at such times that negative values were obtained for this fraction. The methods employed evidently do not give an exact measure of the distribution of the phosphorus fractions, but they do serve to indicate the general magnitudes of the quantities in which each occurs.

The meaning of the particulate and dissolved fractions of organic phosphorus depends upon the properties of the barium sulfate filter. When a suspension of diatoms, *Nitzschia closterium*, containing a known amount of phosphorus is filtered, the phosphorus may be recovered quantitatively from the filter. The refiltration of a filtrate leaves no detectable amount of phosphorus upon the filter. Evidently diatoms and microorganisms of similar size are completely retained in the particulate fraction. Dr. Charles E. Renn has kindly tested the filter for the retention of bacteria. After filtering sea water containing some 400 bacteria per milliliter the filtrate contained about one-sixth that amount. The particulate organic phosphorus fraction probably contains the phosphorus of all the larger phytoplankton and smaller zoöplankton and the greater portion of the bacteria and detritus as well. The dissolved organic phosphorus fraction may include a small

TABLE II

Specimen of data on phosphorus fractions in samples of sea water. Concentrations expressed as milligrams PO_4 per cubic meter.

Depth in meters	I Inorganic phosphorus	II Particulate phosphorus	III Phosphorus in filtrate	IV Total phosphorus II + III	V Total phosphorus. Direct analysis	VI Difference	VII Organic phosphorus III − I
1	45	10	64	74	62		
			70	80	86		
			68	78			
			67	77	71	+ 6	22
10	27	13	64	77	68		
			60	73	86		
			64	77			
			63	76	77	− 1	36
20	39	14	66	80	86		
			70	84	86		
			45	59			
			60	74	86	−12	21
60	110	6	116		130		
					116	− 1	6
				122	123		
100	110	4	126		142		
					142		
				130	142	−12	16
125	115	5	132		138		
					146		
				137	142	− 5	17
					160		
					156		
150	111	5	142	147	158	−11	31
200	123	5	152		154		
					162		
				157	158	− 1	29
225	108	8	148		162		
					158		
				156	160	− 4	40

portion of the bacterial flora, perhaps some minute nannoplankton, and detritus which has been reduced to the smallest dimensions in addition to organic compounds of phosphorus in colloidal form or in true solution. Renn (1937) has estimated that a bacterial population of 100,000 cells per milliliter would represent only 2.9 mg. PO_4 per cubic meter. It is evident that the much larger values of dissolved organic phosphorus obtained in our analyses can be due in only negligible part to the presence of bacteria. We believe, consequently, that our measurements represent chiefly the presence of phosphorus compounds in solution.

TABLE III

Inorganic phosphorus. Concentrations expressed in milligrams PO_4 per cubic meter. Depths not corrected for wire angle, which in no case would reduce by more than 4 per cent.

Depth in meters	May 18 1935	August 21 1935	November 8–9 1935	February 26 1936	May 14 1936
1	35	5	45	105	14
10	28	21	27	102	10
20	34	53	39	103	15
30	59	96	78	99	82
40	70	92	73	100	95
50	—	—	77	96	97
60	97	93	110	88	116
80	105	110	89	99	117
100	108	109	110	95	120
125	114	107	115	99	129
150	122	122	111	96	147
175	138	132	123	131	152
200	146	137	123	141	146
225	161	136	106	143	157
250	170	139		139	

The distribution of phosphorus in the three forms into which it has been separated is recorded in Tables III, IV, V and VI. Inorganic phosphate represents by far the greater quantity of phosphorus in the water amounting to 72 to 92 per cent of the total at different times. It is rather uniformly distributed at depths greater than 80–100 meters throughout the year, the concentrations increasing somewhat with depth. In the superficial layers, as has been frequently observed elsewhere, the inorganic phosphate becomes greatly reduced in quantity in the spring and is restored to concentrations characteristic of greater depths during the winter.

Particulate organic phosphorus, representing organisms and detritus, is in general the smallest of the three fractions, amounting to about 5 per cent of the total. It occurs in greatest quantity in the

upper layers—above 40 meters—corresponding to the observed distribution of phytoplankton (Gran and Braarud, 1935). The quantities in these layers are highest in spring; in midwinter the quantity in surface water is scarcely to be distinguished from that in deep water. The values obtained in August are subject to doubt. Below the photosynthetic zone the distribution of filterable organic phosphorus is on the whole very uniform, amounting to about 5 γ PO_4 per liter. The distribution and magnitude of the concentrations of filterable phosphorus agree well with that of particulate nitrogen observed by von Brand (1937) in these waters in the summer of 1936.

TABLE IV

Particulate organic phosphorus. Concentrations expressed in milligrams PO_4 per cubic meter. Depths not corrected for wire angle, which in no case would reduce by more than 4 per cent.

Depth in meters	May 18 1935	August 21 1935	November 8–9 1935	February 26 1936	May 14 1936
1	20	13	10	6	17
10	18	14	13	5	13
20	15	15	14	5	20
30	20	7	9	4	12
40	12	8	7	4	0
50	—	—	5	4	8
60	5	5	6	6	9
80	8	6	4	4	12
100	5	5	4	4	3
125	4	3	5	3	2
150	3	—	5	3	3
175	5	3	13	3	1
200	4	3	5	3	7
225	4	4	8	4	7
250	6			5	

In May dissolved organic phosphorus occurred in only minimal quantities in the water of all depths except near the surface. During the summer the concentration increases markedly until November, when over 20 per cent of the total phosphorus is in this form. In the early winter there is a rapid disappearance of this form of phosphorus, associated in time with the increase in concentration of inorganic phosphate in the upper waters. The appearance of organic phosphorus commences in May at the surface, and the concentrations appear to grow from the surface downward. Not until November are high concentrations observed near the bottom. These observations suggest that considerable decomposition is taking place throughout the water column and in particular in those depths where phyto- and zoöplankton

are known to exist in greatest numbers; and that at this station decomposition at the bottom may be relatively unimportant. The findings concerning organic phosphorus are somewhat similar to those of Kreps and Osadchik (1933), who made studies in Barents Sea. They found organic phosphorus to show a gradual increase from August to January reaching concentrations of some 40 mg. P_2O_5 per cubic meter and actually exceeding the inorganic phosphorus during the latter month. Their observations, which did not cover the earlier part of the year, showed the greatest concentrations in the deeper waters. As will be pointed out in a subsequent publication, the seasonal distribution of soluble organic phosphorus has some resemblance to

TABLE V

Dissolved organic phosphorus. Concentrations expressed in milligrams PO_4 per cubic meter. Depths not corrected for wire angle, which in no case would reduce by more than 4 per cent.

Depth in meters	May 18 1935	August 21 1935	November 8–9 1935	February 26 1936	May 14 1936
1	30	49	21	− 2	12
10	15	36	35	0	0
20	−1	50	29	22	35
30	−4	14	7	14	18
40	3	24	36	− 3	3
50	—	—	43	5	3
60	8	36	7	1	26
80	0	24	50	9	55
100	2	30	24	21	22
125	−3	29	20	21	22
150	2	6	38	22	9
175	−6	20	20	4	−11
200	−7	22	30	6	8
225	−2	17	43	− 4	10
250	8			−10	

that of ammonia, which may be considered to be a somewhat analogous stage in the nitrogen cycle.

The data recorded in Tables III, IV and V have been submitted to further analysis with a view to determining in so far as possible, just what alterations take place in the phosphorus cycle at various depths and at different times of year.

The column of water is considered to be virtually a closed system in which every exchange with the surroundings is exactly balanced by an equal and opposite exchange. By dividing the column into a number of segments lying at different depths, in which the quantity of phosphorus in the different forms is recorded from time to time, and by

observing certain general biological and hydrographic principles, it becomes possible to estimate to what extent changes in the concentrations of each form of phosphorus may be derived from processes taking place in situ, and to what extent vertical movements of phosphorus from one segment or layer to another must be postulated.

To obtain a workable body of data, Table VI has been drawn up recording the quantity of phosphorus present in each of the three

TABLE VI

Summary of distribution of phosphorus fractions.

	Depth in meters	May 18 1935	Aug. 20 1935	Nov. 8 1935	Feb. 26 1936	May 14 1936
Total P as grams PO_4 per sq. m.	0–240	28.7	31.0	32.9	29.9	34.4
Percentage of total phosphorus in each 60-meter layer	0–60	16.4	20.6	18.0	22.0	14.9
	60–120	23.7	23.2	25.0	23.0	28.0
	120–180	27.0	26.3	28.0	25.0	27.9
	180–240	32.9	29.9	29.0	30.0	29.2
	Total	100.0	100.0	100.0	100.0	100.0
Inorganic phosphorus as percentage of total	0–60	11.9	12.6	11.3	19.7	10.6
	60–120	22.1	16.8	18.7	19.4	20.8
	120–180	26.0	22.5	21.6	21.1	25.0
	180–240	32.0	25.6	21.2	28.7	26.5
	Total	92.0	77.5	72.8	88.9	82.9
Dissolved organic phosphorus as percentage of total	0–60	1.5	6.2	5.0	1.4	2.3
	60–120	0.4	5.4	5.4	2.7	6.0
	120–180	0.2	3.2	5.0	3.3	2.5
	180–240	0.0	3.7	6.4	0.6	1.7
	Total	2.1	18.5	21.8	8.0	12.5
Particulate organic phosphorus (organisms and detritus) as percentage of total	0–60	3.0	1.8	1.7	0.9	2.0
	60–120	1.2	1.0	0.9	0.9	1.2
	120–180	0.8	0.6	1.4	0.6	0.4
	180–240	0.9	0.6	1.4	0.7	1.0
	Total	5.9	4.0	5.4	3.1	4.6

forms for each of four layers each of 60 meters depth at each time of observation. The values are obtained by graphical integration and are expressed as percentages of the total phosphorus in a water column of 240 meters depth at each time of observation. In analyzing these data the following premises are held:

1. *The horizontal exchange due to the drift of water past the station may be neglected.* This premise is not justified on the ground that the

station is located in a region of minimal drift. There can be little doubt that water is constantly drifting past the station. The observed changes in salinity demonstrate this. The total phosphorus recorded varies ± 7 per cent from the mean value throughout the year. Since this variation shows no seasonal sequence, the total phosphorus being lowest in May, 1935 and maximal in May, 1936, there evidently is some variation in the character of the water occupying the station at different times. These differences are eliminated by expressing the phosphorus fractions as percentages of the total, a procedure which imposes artificially the character of a closed system upon the set of data. The justification of this procedure lies in the relatively small differences in total phosphorus observed from time to time, and in the fact that on the whole the horizontal distribution of phosphorus throughout the Gulf at any time, at least to judge by inorganic PO_4, is much more uniform than is the vertical distribution. The horizontal distribution of PO_4 at various depths throughout the Gulf as observed in May, 1934 are shown in Fig. 4 and illustrate this fact. The general character of the phosphorus cycle may be supposed to be similar in all parts of the basin.

2. *Phosphate present as zoöplankton and nekton and not sampled by the water bottle may be ignored.* A large number of vertical zoöplankton hauls made throughout the years 1933–34 in all parts of the Gulf yielded an average catch of 40 cc. dry plankton per square meter of surface. It may be estimated from analyses made on such material that this would contain about 0.4 per cent of the total phosphorus in the water from which it was strained. Since the particulate organic phosphorus amounts to about ten times this quantity, it may be seen that the neglect of this fraction does not introduce a significant error.

3. *All synthesis of particulate or soluble organic phosphorus compounds from inorganic phosphate takes place in the upper layer.* This is justified by Clarke's measurements on the penetration of light into the Gulf of Maine and on determinations of the compensation point in photosynthesis by diatoms in bottle experiments at different depths (Clarke and Oster, 1934).

4. *All downward movement of phosphorus is due to the sinking of organisms (particulate organic phosphorus).* This is the only fraction affected by gravity. It is also the only fraction displaying a well-marked concentration gradient decreasing downward—a condition essential for downward dispersal by eddy conductivity.

5. *All upward movement of phosphorus is due to the transport of inorganic PO_4 by eddy conductivity.* The gradient of concentration of inorganic PO_4 increases downward and is well marked except in mid-

winter. The soluble organic phosphorus never develops a strong gradient in this direction. Since it is present in much smaller concentrations than is the inorganic phosphate, it may safely be ignored in considering vertical transport by eddy conductivity.

6. *All observed transformations in any layer are attributed to processes occurring in that layer, except so far as vertical transport must be postulated to account for the transformation.* This premise is introduced since without it a unique solution cannot be obtained. It implies that all values arrived at for vertical exchange are minimal.

7. *The portion of the exchange in which the cycle runs to completion is necessarily ignored. All values for the magnitude of the exchange are consequently minimal.*

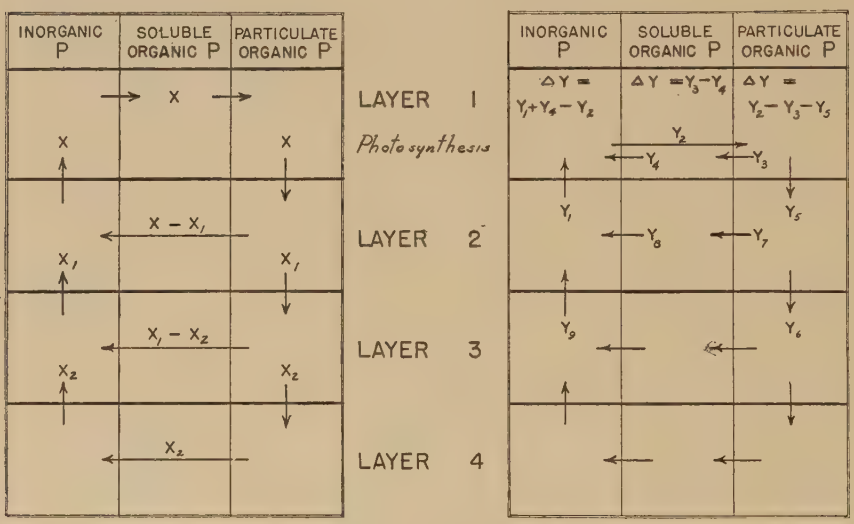

FIG. 2. See text.

A consideration of this limitation may serve to make clear the general basis of the analysis. If we start with the system in a steady state and if, during the period between two sets of observations the cycle has proceeded without change in the relative velocity of the processes in any part, the distribution of the fractions of phosphate in all parts of the system will be the same at the end as it was in the beginning. This does not mean that no exchanges of phosphate between different parts of the system have taken place, rather that all exchanges are exactly compensated. While the system is in a steady state an unobservable quantity of phosphate is undergoing transformation from each stage in the cycle to the next stage. If the system is disturbed, as through seasonal changes in the physical conditions, then

transformations of one sort may proceed more rapidly than those of another with the result that differences in the distribution of phosphorus are observed, and from these differences the magnitude and nature of the processes *which have caused* the differences may be deduced. The observations tell us nothing, however, of the basal level of activity on which the differences are superposed.[2]

Figure 2 illustrates the principle of the method. At any time there will be a basal level of activity represented by the transformation of an unobservable quantity of phosphorus, x, through each stage in the cycle. This quantity will have been transported upward from layer 2 into layer 1 to be synthesized into particulate organic form. If the system is to remain unchanged, the equivalent of this material must have sunk back into the deeper layers and been decomposed, passing through the soluble organic form, to exactly replace that which was transported upward. Portions of x, designated as x_1, x_2, etc. may sink to deeper layers before undergoing transformations from organic to inorganic form. The general conditions are that the quantity of x entering and leaving any part of the system shall be equal, that x move upward as inorganic phosphate (Postulate 5), and downward as filterable organic phosphorus (Postulate 4), that it represent synthesis of filterable organic phosphorus only in the upper layer, and that it represent a transformation of organic into inorganic phosphorus in any layer.

If the system is disturbed between observations, then changes in the quantity of phosphorus, ΔY, in any form and part of the system may be observed. These changes may be accounted for only by additional exchanges between the various parts of the system. The problem is to determine the minimal additional exchanges of this sort, Y_1, Y_2, Y_3 etc., which will account for the change in each part of the system in accordance with the postulates laid down above. The general conditions are that ΔY, the change in any fraction in any layer shall equal the difference in Y_1, Y_2, Y_3 etc., the amounts of phosphorus entering or leaving that fraction and layer during the period between observations. Furthermore, ΔY must be accounted for so far as possible by exchanges taking place within the layer in question (Postulate 6).

An attempted analysis of the changes in phosphorus distribution is presented in Tables VII, VIII and IX.

February to May (Table VII) represents the period in which the

[2] The method is analogous to the integration of a differential equation, the unobserved basal activity corresponding to the constant of integration. It is only in proportion as the system undergoes great seasonal fluctuation that the partial effects observed approach the total exchanges taking place. The method is applicable consequently particularly to studies made in high latitudes.

great spring flowering of phytoplankton occurs. During this period an amount of phosphorus equivalent to 9.1 per cent of the total disappears from the inorganic phosphate of the upper layer. Of this only 2.0 per cent can be accounted for as an increase in particulate and soluble organic phosphorus remaining in that layer. Seven and one-tenth per cent must have sunk to the deeper layers following its synthesis into organic matter. Only one-eighth of the phosphorus absorbed in

TABLE VII

Balance sheet of phosphorus exchanges February 26 to May 14, 1936. Numbers represent the change in the phosphorus fractions as percentages of total phosphorus in water column.

Depths		Inorganic phosphorus	Soluble organic phosphorus	Particulate organic phosphorus
0–60 meters	Photosynthesis	−9.1	→	+9.1
	Decomposition		+0.9 ←	−0.9
		0 ←	0	
	Exchange with layer below	0	0	−7.1
	Net change	−9.1	+0.9	+1.1
60–120 meters	Exchange with layer above	0	0	+7.1
	Decomposition		+4.7 ←	−4.7
		+1.4 ←	−1.4	
	Exchange with layer below	0	0	−2.1
	Net change	+1.4	+3.3	+0.3
120–180 meters	Exchange with layer above	0	0	+2.1
	Decomposition		+0.9 ←	−0.9
		+1.7 ←	−1.7	
	Exchange with layer below	+2.2	0	−1.4
	Net change	+3.9	−0.8	−0.2
180–240 meters	Exchange with layer above	−2.2	0	+1.4
	Decomposition	0	+1.1 ←	−1.1
	Net change	−2.2	+1.1	+0.3

photosynthesis has remained as particulate matter in the upper layer. This observation accords with the conclusion of Harvey (1934) that several times more vegetation is produced during the spring flowering of diatoms in the English Channel than is found there at the time of its maximum.

To account for the increasing concentrations of inorganic phosphorus in the deeper layers after allowing for the greatest possible decomposition in situ at least 2.1 per cent must sink past the 120-meter

level and 1.4 per cent past the 180-meter level. The phosphorus removed from inorganic form in the upper layer by photosynthesis is redistributed during the spring through considerable depths by the sinking of particulate matter. It is unnecessary to assume that any of the particulate matter sinks beyond the lower level before undergoing decomposition, though it is possible that this may be the case.

May to November (Table VIII) includes the greater part of the

TABLE VIII

Balance sheet of phosphorus exchanges May 18, 1935 to November 8, 1935. Numbers represent the change in the phosphorus fractions as percentages of total phosphorus in water column.

Depths		Inorganic phosphorus	Soluble organic phosphorus	Particulate organic phosphorus
0–60 meters	Photosynthesis	−19.2	→	+19.2
	Decomposition		+3.5 ←	−3.5
		0 ←	0	
	Exchange with layer below	+18.6	0	−17.0
	Net change	−0.6	+3.5	−1.3
60–120 meters	Exchange with layer above	−18.6	0	+17.0
	Decomposition		+5.0 ←	−5.0
		0 ←	0	
	Exchange with layer below	+15.2	0	−12.3
	Net change	−3.4	+5.0	−0.3
120–180 meters	Exchange with layer above	−15.2	0	+12.3
	Decomposition		+4.8 ←	−4.8
		0 ←	0	
	Exchange with layer below	+10.8	0	−6.9
	Net change	−4.4	+4.8	+0.6
180–240 meters	Exchange with layer above	−10.8	0	+6.9
	Decomposition		+6.4 ←	−6.4
		0 ←	0	
	Net change	−10.8	+6.4	+0.5

growing season. The important feature of this period is the appearance of large quantities of dissolved organic phosphorus at all depths. One-fifth of all the phosphorus in the water is in this form in November. This material can have been produced only by photosynthetic processes taking place in the upper layer. It must have been set free for the most part by decomposition of the particulate fraction in the layer in which it is observed (Postulate 5). In order to account for the

quantities of dissolved organic phosphorus observed, a large vertical movement of inorganic phosphorus upward through all depths must be postulated as well as an equivalent sinking of organisms to the sites at which the soluble organic phosphate appears. Over 17 per cent of the total phosphorus in the water must pass through the zone of photosynthesis in the course of the six summer months. Since the account is balanced without supposing any phosphorus to pass from the organic

TABLE IX

Balance sheet of phosphorus exchanges November 8, 1935 to February 26, 1936. Numbers represent percentages of total phosphorus in entire water column.

Depths		Inorganic phosphorus	Soluble organic phosphorus	Particulate organic phosphorus
0–60 meters	Photosynthesis	0	→	0
	Decomposition		+0.6 ←	−0.6
		+4.2 ←	−4.2	
	Exchange with layer below	+4.2	0	−0.2
	Net change	+8.4	−3.6	−0.8
60–120 meters	Exchange with layer above	−4.2	0	+0.2
	Decomposition		0 ←	0
		+2.7 ←	−2.7	
	Exchange with layer below	+2.2	0	−0.2
	Net change	+0.7	−2.7	0
120–180 meters	Exchange with layer above	−2.2	0	+0.2
	Decomposition		0 ←	0
		+1.7 ←	−1.7	
	Exchange with layer below	0	0	−1.0
	Net change	−0.5	−1.7	−0.8
180–240 meters	Exchange with layer above	0	0	+1.0
	Decomposition		+1.7 ←	−1.7
		+7.5 ←	−7.5	
	Net change	+7.5	−5.8	−0.7

back to the inorganic form, a process which must certainly be taking place, this figure may be far below that actually obtaining.

November to February (Table IX) is marked chiefly by the regeneration of inorganic phosphorus, which increases by 16 per cent of the total, and by the equalization of the concentration of this fraction throughout the water column. The table shows that this regeneration is made to a large extent at the expense of the soluble organic phos-

phorus, that the transformation takes place throughout the entire range of depths, though greatest near the bottom. The decomposition of organic phosphorus compounds in situ and the vertical transport of inorganic phosphate are about equally important in effecting the equalization of the concentration of the latter throughout the water column.

The Mechanism of Vertical Transport

The foregoing analysis indicates that very considerable exchanges of phosphorus take place between various depths of water. At the same time these exchanges appear to diminish in extent as the depth increases. Downward movement has been attributed to the sinking of particulate matter under the influence of gravity. There appears to be no difficulty in considering that in depths of a few hundred meters organized particles of the dimensions of diatoms would sink to the bottom before undergoing decomposition. If such were the case very large quantities of phosphorus would be withdrawn from the water during each growing season. This may be the case in shallow waters, but it does not appear to be happening in the western basin of the Gulf of Maine. If so the total phosphorus in the water should show a marked seasonal change. The situation is probably complicated by biological considerations. Harvey (1934) has presented evidence that the stock of phytoplankton is grazed down by zoöplankton during the summer. This conclusion suggests that the zoöplankton are important active agents in converting particulate organic phosphorus into its decomposition products. Since these animals, and particularly the copepods, make extensive diurnal vertical migrations, and since some time must elapse between the taking of food near the surface and its elimination as waste products, they provide an agency for a limited vertical transport of organic material. From this viewpoint the zoöplankton become an important agency in maintaining the fertility of the water for phytoplankton, since they hasten the conversion of bound nutrients into inorganic form and prevent these nutrients from becoming unavailable by the sinking of particulate matter to great depths or to the bottom.

The vertical transport of inorganic phosphate is simpler since it can be effected only by the mixing of the water. It is pertinent to inquire whether the conditions are such as to permit of the amounts of transport deduced during the various periods of observation. The amount of a constituent, Q, passing through unit horizontal surface in unit time depends upon the gradient of concentration of the constituent

dc/ds and the coefficient of eddy conductivity, A (Austausch coefficient).

$$Q = A\,dc/ds$$

The coefficient of eddy conductivity, A, represents the volume of water exchanged through each horizontal unit surface in unit time.

The gradient of phosphate concentration observed in February, May and November is shown in Fig. 3. Between May and November, when large vertical movements have been deduced, a well-marked gradient exists particularly in the upper layers, as is required for such movements. In February this gradient has disappeared, and the

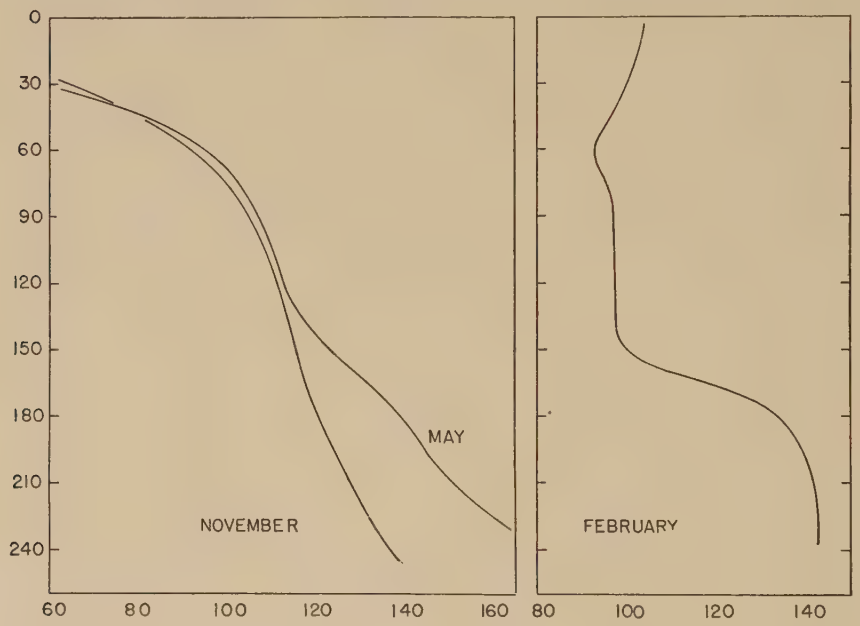

FIG. 3. Distribution of inorganic phosphate concentration with depth in November, 1935 and February and May, 1936 at standard station in the western basin of the Gulf of Maine. Depths in meters measured downward along the ordinate; concentrations in milligrams PO_4 per cubic meter along the abscissa.

concentration of phosphate is equal at all depths down to 150 meters. No amount of mixing can effect a change in its vertical distribution. Since this condition must exist during a considerable portion of the winter, it is not surprising that the vertical transports *deduced from our data* between November and May are smaller than those observed in the summer.

A knowledge of the coefficient of eddy conductivity, A, is the key to understanding the nutritive conditions in deep bodies of water.

Methods of estimating its value are so indirect that little is known of its magnitude under any circumstances. Although our data are admittedly very unprecise and yield only minimal values for the exchange, it is nevertheless of some interest to use it in estimating the coefficient required to account for the transport of phosphate in the Gulf of Maine. The gradient of phosphate concentration is sufficiently uniform throughout the period May–November to permit a single value to be taken at any level as representative of the entire period. This is not the case during the remainder of the year. We have

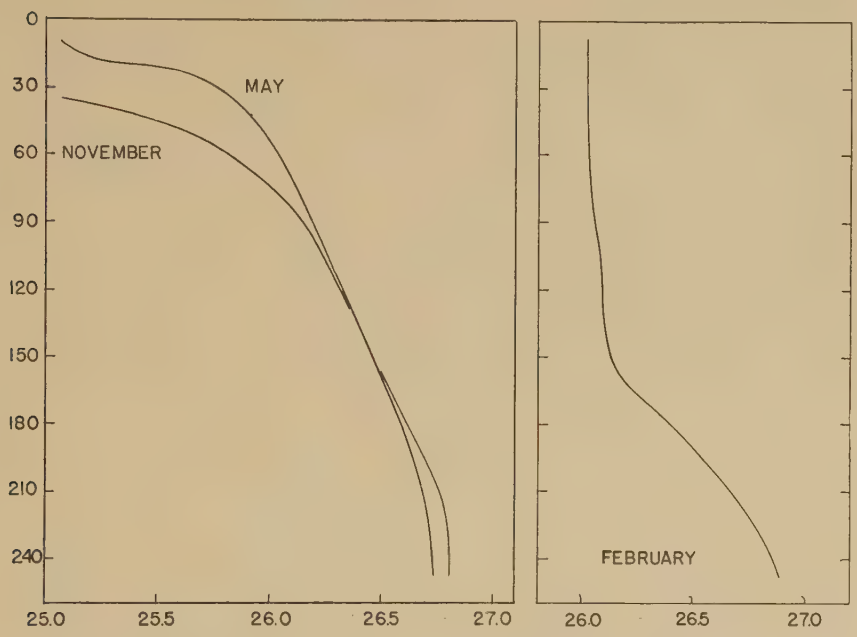

FIG. 4. Distribution of density, σ_t, with depth in November, 1935, and February and May, 1936, at standard station in the western basin of the Gulf of Maine Depths in meters measured downward along the ordinate; density, σ_t, measured along the abscissa.

calculated the value of A for the boundary of each of the layers, using the data presented in Table VIII for estimating Q and the slopes of the curves in Fig. 3 for dc/ds. The result is shown in Table X. The values of A are minimal and are less reliable at the greater depths. The values obtained are not unreasonable. Seiwell considered A to equal 2 C.G.S. units in the thermocline of the tropical Atlantic, whereas values increasing to 50 C.G.S. units have been obtained in various waters (Seiwell, 1935).

The value of the coefficient of eddy conductivity depends upon the forces responsible for mixing and varies inversely with the stability, $\frac{d\sigma_t}{ds}$ of the water. If K represent the mixing forces,

$$K = A \times \frac{d\sigma_t}{ds}$$

Seiwell considers that $K = 4.73 \times 10^{-4}$ in the thermocline of the North Atlantic. Figure 7 shows the distribution of density, σ_t, with depth at the station in the Gulf of Maine in May, 1935 and in November. From these curves the representative values of $\frac{d\sigma_t}{ds}$ entered in Table X are taken. The values of K given by multiplying $\frac{d\sigma_t}{ds}$ by A are of the order obtained by Seiwell. It is concluded that the

TABLE X

Estimation of coefficient of eddy conductivity in Gulf of Maine, May to November, 1935.

Depths	Q		dc/ds	A	$d\sigma_t/ds$	$K = A \times \frac{d\sigma t}{ds}$
meters	*per cent in 3 months*	$\frac{mg.}{cm.^2 \times sec.}$	$\frac{mg.}{ml.\ cm.}$	$\frac{ml.}{cm. \times sec.}$	$\frac{grams}{ml. \times cm.}$	
60	>18	$>3.5\times10^{-8}$	6.6×10^{-9}	> 5.2	1.0×10^{-4}	$>5.2\times10^{-4}$
120	>15	$>2.4\times10^{-8}$	2.0×10^{-9}	>12.0	0.5×10^{-4}	$>6.0\times10^{-4}$
180	>10	$>2.0\times10^{-8}$	3.0×10^{-9}	> 6.6	0.4×10^{-4}	$>2.6\times10^{-4}$

vertical transport of inorganic phosphate deduced from the seasonal change in the distribution of the various fractions of phosphorus compounds does not require unreasonable assumptions concerning the magnitude of the eddy conductivity.

SUMMARY

1. Methods are described for the determination of the phosphorus present in particulate form and of the total phosphorus in a sample of sea water.

2. The distribution of phosphorus present as inorganic phosphate, as dissolved organic compounds, and as particulate matter (detritus and microörganisms) has been determined at all depths throughout the year at a station in the western part of the Gulf of Maine.

3. In late winter over 90 per cent of the phosphorus is in inorganic form and three-quarters of the remainder is present as soluble organic compounds.

4. In the spring—February to May, inorganic phosphorus is converted to organic form by photosynthesis in the upper layer of water. Most of this fraction sinks to considerable depths before undergoing decomposition.

5. During the summer—May to November, large quantities of dissolved organic phosphorus appear at all depths, indicating a very considerable transport of inorganic phosphate from deep water to the surface and the sinking of an equivalent amount of phosphorus in particulate form to the depths in which organic compounds are liberated by decomposition. Decomposition appears to take place throughout the water column.

6. During the winter—November to February, the organic phosphorus compounds are converted to inorganic phosphate. This and vertical mixing of preformed phosphate are about equally important in bringing about the equalization of phosphate concentrations throughout the depth of water.

7. A method is described for analyzing quantitatively the factors producing a seasonal change in the distribution of a compound such as phosphorus. It is shown that the vertical transport of material within the water mass demanded by such an analysis may be accounted for reasonably by the hydrographic conditions obtaining.

8. Values of the coefficient of eddy conductivity at several depths are obtained.

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THE EXPERIMENTAL DECOMPOSITION AND REGENERATION OF NITROGENOUS ORGANIC MATTER IN SEA WATER [1]

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Historical

Although the formation of nitrate from composted nitrogenous organic materials has been long known and practically applied, the current conception that specific biological agencies bring about these natural processes in soils, fresh waters, and the sea was developed only in the last quarter of the nineteenth century. In his studies on acetic acid fermentation Pasteur (1862) anticipated the rôle of bacteria in the ultimate oxidation of ammonia to nitrate, but Schloesing and Müntz (1877 et seq.) first demonstrated the biological nature of the intermediaries. The demonstration was performed in soils; Müntz, shortly afterward (1890), showed that ammonia was produced in soils by microbial breakdown of proteinaceous organic matter. That the oxidation of ammonia to nitrate proceeded through nitrite was distinguished by Munro (1886), but not until Winogradsky (1891, 1892) performed his classic researches were the two oxidations recognized as separately determined by specific ammonia-oxidizing and nitrite-oxidizing bacteria.

Following these researches Adeney (1895) demonstrated the complete sequence of nitrate regeneration in natural and sewage polluted water, establishing the steps by clear-cut quantitative methods. His procedures determined the basis for standard sewage analysis.

It has been held by Brandt (1899, 1902) and many others that the cycle of nitrogen in the sea follows essentially the same phases, and, using this interpretation, a number of researches into the occurrence and distribution of specific marine organisms have been made. These investigations have been reviewed and extended by Waksman, Hotchkiss and Carey (1933). There is considerable conflict in the literature on biological nitrification in the sea, but the conventional picture derived from studies of soils and fresh waters is nevertheless applied to oceanographic chemical data.

[1] Contribution No. 129 of the Woods Hole Oceanographic Institution.

Experimental

Because of the growing interest in the regeneration of nitrate in the sea it seemed highly desirable to make a quantitative investigation of the course of organic decomposition and of the simultaneous appearance of nitrogenous products in the water. To this end, a number of experiments were carried out in which a natural source of organic matter—plankton material from customary net-hauls—was allowed to rot and

Table I

Series I. Source of organic matter: mixed plankton tow.
Micrograms of nitrogen per liter.

Date	Plankton	In water					Total in system ‡	Dissolved organic N	Bacteria in thousands per ml.
		Ammonia	Nitrite	Nitrate + nitrite	Nitrate	Total in water			
6–27....	188	0	0	5	5	5	193	150	100
29....	150								160
30....		80	0	5	5	85			204
7– 2....	131	107	0.1	5	5	112	243		180
5....	110	160	3.8	6	2	166	276		123
10....	82						277		
11....		185		10		195			22
15....			2.4						
17....	77						308		40
18....		225	2.7	6	3	231			
24....	40		16				272		
25....		200		32		232			20
27....			55	70	15				
28....		185	80	90	10	275			
30....		125	110	145	35	270			36
8– 1....		60	180	215	35	275			
5....		11	150	275	125	286			
7....	47	0	110	300	190	300	347		
10....		8	2.2	300	298	308			
8–11*....		Portion inoculated with diatoms							
19....	285	0	0	20	20	20	305		
22....	300	0		13	13	13	313		
8–11*....		Control portion, not inoculated							
12....			0.5	360	360				
14....				330					
17....			0.6	330	330				
19....	37	0		360	360	360	397	200	
21....			0.8	330	330				
22....		0							

* One portion inoculated with diatoms and placed in the light.
‡ Does not include dissolved organic nitrogen.

decompose in sea water. Observations were made to follow the disappearance of nitrogen in the decomposing material and its appearance in the water in the form of ammonia, nitrite and nitrate, in the effort to reproduce artificially the cycle of organic decomposition and eventual regeneration. If, by means of the soluble compounds resulting from the decomposition, the water could be rendered fertile and capable of

TABLE II

Series II. Source of organic matter: mixed plankton tow.
Micrograms of nitrogen per liter.

Date	Plankton	In water					Total in system ‡	Dissolved organic N	Bacteria in thousands per ml.
		Ammonia	Nitrite	Nitrate + nitrite	Nitrate	Total in water			
7–12....	400	18	0.2	8	8	26	426	420	82
14....	345								176
15....		>120	0.5	8	8				265
17....	275	>120	0.2	6	6				270
20....	202	550	2.3	8	6	558	760		80
23....		580							
24....			16						43
25....		600		27		627			
27....			60	80	20				
28....		650	110	150	40	800			25
29....	90								
30....		550	240	300	60	850	940		
8– 1....		340	550	590	40	930			16
5....		12	800	820					
7....	78	4	850		60	914	992		
8....				910					
10....		8	550	1000	450	1000			20
12....			190	1100	910	1100			
14....		35	0.1	1050	1050	1100			25
17....			0.1	1100	1100				
18....	133						(1250)		
8–21*....		Portion inoculated with diatoms							
27....	305								
28....			1.0						
31....	840		7.7	320	312	(330)	(1170)		
9– 2....	1010		0	25	25	(35)	(1045)		
3....								470	
8–21*....		Control portion, not inoculated							
22....		7	0.5						
28....			0.3	1050	1050				
29....				1000					
31....			0.5						

* One portion inoculated with diatoms and placed in the light.
‡ Does not include dissolved organic nitrogen.

supporting a new organic growth, comparable to that previously decomposed, the complete cycle would have been carried out. It was also hoped that periodic chemical analysis, by methods now available, might throw light on the sequence of the various steps in the cycle.

The raw material was mixed plankton, collected in the usual way in a No. 20 net, quickly washed, and kept on ice for the few hours before it could be returned to the laboratory. This material was then suspended in 10–15 liters of fresh, filtered sea water and stored in the dark at a temperature of 20–25° C.

Several different analyses were carried out on this material at the start and at intervals thereafter, the various fractions being determined as follows:

1. Total nitrogen contained in the suspended or particulate matter. This is called "plankton nitrogen" in the following descriptions, but also includes bacterial nitrogen as well as that in any other form of suspended matter. This determination follows the procedure described by von Brand (1935) and consists essentially of precipitating the

TABLE III

Series IV. Source of organic matter: mixed plankton tow, strained through No. 8 bolting silk. Micrograms of nitrogen per liter.

Date	Plankton	In water					Total in system *	Bacteria in thousands per ml.
		Ammonia	Nitrite	Nitrate + nitrite	Nitrate	Total in water *		
7–28	115	43				55	170	152
29			0.6	12	12			200
30	83	110						305
8– 1	63	150	1.0	15	14	165	228	190
5	38	205	<1	10	10	215	253	35
7		190	0.6	10	10	200		16
10	40	200		15	15	215	255	
14		240	0.5	20	20			25
17	41			17	17			
20			13					
21				35				20
22		210	21			(250)		18
27	58	175	120	140	20	315	373	
29			190					
31		29	220	240	20	269		
9– 2		25	225	225	(0)	250		
5	59							
8				260				
14		14	310	330	20	344	(400)	
27			130	290	160			
10–4			1					

* Does not include dissolved organic nitrogen.

suspended matter in a sample of the water by the addition of alkali. The precipitate drags down all suspended and colloidal matter, and after settling and centrifugation is separated and resuspended. The resulting small volume of suspension is then used for a determination of total nitrogen by the method of Krogh and Keys (1934): fusion with KOH in a stream of hydrogen, followed by recovery of the ammonia.

2. Ammonia in the water, by a slight modification of the method of Krogh (1934), in which the original design of the still was changed somewhat, to make it more compact and to permit heating electrically.

3. Nitrite in the water by the well-known Griess-Ilosvay method.

4. Nitrate (including nitrite) in the water, by Harvey's reduced

TABLE IV

Series VI. Source of organic matter: washed, persisting culture of *Nitzchia*. Micrograms of nitrogen per liter.

Date	Plankton	In water					Total in system *
		Ammonia	Nitrite	Nitrate + nitrite	Nitrate	Total in water *	
8–14			0.1				
15	633	2		17	17	19	652
18	514	120	0.1	15	15	165	679
21	430	230	0.1	16	16	246	676
27	298	310	0.4	24	24	334	632
9– 2	201	410	1.3	20	19	430	631
8	226			25	25		
14		490	0.1	17	17	507	(700)
27			0.2	20	20		

* Does not include dissolved organic nitrogen.

strychnine method. Nitrate then calculated by subtracting the value of nitrite as obtained under 3.

5. Bacterial counts.

The data from the chemical analyses are collected in Tables I to IV and some of them are also presented graphically in Figs. 1 and 2.

Several different "series" were carried out: I, II and IV, in which the organic material was a mixed tow of both phyto- and zoöplankton, of varying amount in each case; and VI, in which a persisting washed culture of diatoms was used as the source of organic matter. In Series II the sea water in which the plankton was suspended came from the surface of Woods Hole Harbor, which probably accounts for its higher content of dissolved organic nitrogen than that of the water in

the other series, which was obtained from the surface a few miles to the south of Marthas Vineyard.

Chemical

The rate of decomposition of the plankton varied in the different series, but after an interval of from 8 to 20 days decomposition stopped. At this time there was still a constant and not inconsiderable amount of nitrogen still remaining, either in non-decomposable plankton residues, bacterial cells, or in other forms. The amount of this residual nitrogen was from 20 to 35 per cent of that originally determined in the plankton, or 7 to 10 per cent of that calculated by addition of the different soluble and insoluble nitrogen fractions.

The rate of decomposition is greatest in the first few days. In Series II, IV and VI it dropped rather suddenly, but in Series I it fell gradually over a longer period of time.

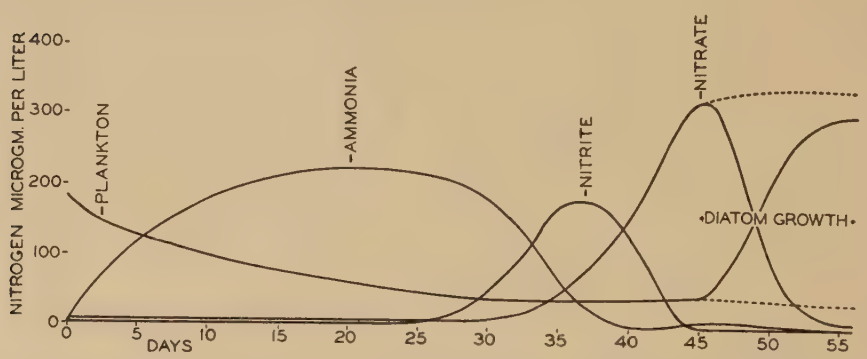

Fig. 1. Series I. The decomposition of nitrogenous organic matter in mixed plankton, showing the appearance of soluble nitrogen compounds in the water in which it is suspended. One portion inoculated with diatoms on the forty-fifth day.

Ammonia appeared in the water rapidly and immediately at the beginning of the decomposition. Evidently the liberation of ammonia is involved in the very first steps in the degeneration of organic matter. It appears more slowly as time goes on, and reaches a maximum when the plankton decomposition ends. During this time there is no rise in the nitrite or nitrate in the water.

The disappearance of ammonia is accompanied by the appearance of nitrite in the water, and this in turn is eventually oxidized to nitrate. The phase during which nitrite was present was 15–20 days in Series I and II, but extended to 40 days in Series IV. In any event, it is not until nitrite reaches its maximum and starts to disappear that nitrate increases.

Eventually, however (after 45 days in Series I, 40 days in II, and 65 days in IV), all the available nitrogen was oxidized to nitrate. At this point, in both Series I and II, a portion of the water was placed in the light and inoculated with fresh diatoms, which grew rapidly, raising the "plankton nitrogen" again and lowering the nitrate to its original minimal value. In this way the complete cycle was carried out.

The question of the existence of soluble nitrogen compounds intermediate between plankton material and ammonia could not be definitely answered, but there was no evidence of any such. Anything in the nature of colloidal cell-material, partially decomposed, must have been carried down in the precipitation and determined with the rest of the plankton nitrogen.

In the transformation of ammonia to nitrite and nitrate it seems that we are dealing not with an equilibrium of simultaneous processes but with distinct, consecutive steps, each doubtless determined by its own set of conditions.

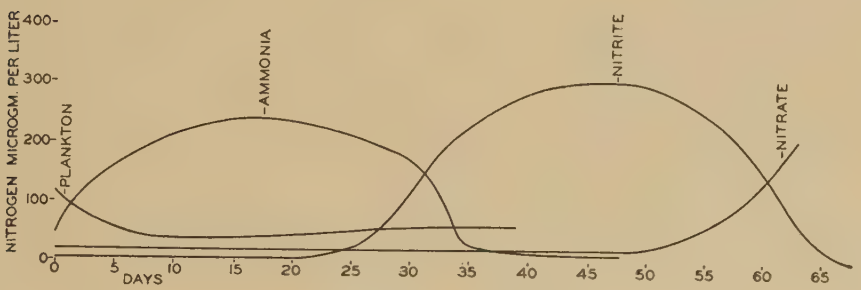

FIG. 2. Series IV. The decomposition of nitrogenous organic matter in mixed plankton, showing the appearance of soluble nitrogen compounds in the water in which it is suspended. Plankton previously filtered through No. 8 bolting silk.

A peculiar situation is revealed by the data from Series I, II and IV. The analyses indicate a larger amount of nitrogen regenerated in soluble forms in the water than that lost by the plankton during decomposition. In the tables the "total nitrogen in the system" has been calculated by addition of all the separate forms determined. This total shows in general a continuous increase throughout the decomposition, especially in Series II. That it is not observed in Series VI may be in some way connected with the fact that the organic material in this case consisted of diatoms.

There are three possible explanations for this nitrogen discrepancy:

1. Participation of other forms of nitrogen in the cycle—most plausibly the dissolved organic nitrogen in the water.

2. Systematic errors in either the sampling procedure or the analytical method, so that the values for plankton nitrogen are regularly too low.

3. Nitrogen fixation.

Each of these possibilities has been critically examined and at the present time none of them seems an altogether acceptable explanation. Determinations of the dissolved organic nitrogen in the water, by the method of Krogh and Keys, did not show any significant change during the experiments. Filtering out the larger plankton organisms in Series IV, to lessen the chance of irregular sampling, had no effect. On the other hand, it is true that the decomposition of very much more finely divided organic matter (diatoms) in Series VI yielded only an equivalent amount of ammonia, but this experiment had to be stopped before nitrification began, which is usually the time when the most pronounced difference between added and recovered nitrogen appears.

According to currently accepted views of biological fixation of nitrogen the third possibility seems doubtful.

A further study of this nitrogen discrepancy is now under way.

Bacteriological

The regeneration of inorganic nitrogen from its various organic forms in plankton proceeds through four recognizable stages, each of which is incident to the development and activity of a special bacterial flora. Following the death of plankton organisms, brought about in these experiments by handling, unfavorable temperatures, lack of illumination, crowding, and inadequate nutrient supply, the more labile components of the dead cells undergo hydrolytic cleavage, simultaneously liberating a fraction of the amino nitrogen as ammonia. This breakdown, it would appear from the rate at which ammonia appears and plankton nitrogen diminishes, is not analogous to the digestion of protein by higher animals where individual protein complexes are first split into smaller molecules bearing amino nitrogen.

A part of the decomposition may be autolytic, but it is evident from the tables, which show an attending rapid development of various species of bacteria, that these organisms must play a large part. The absolute numbers are never very high—in fact, not greater than would be expected in freshly taken, unfiltered sea water stored for such intervals of time (Waksman and Renn, 1936; ZoBell and Anderson, 1936). The decline in plankton nitrogen is not so precipitous as the decrease in bacterial numbers. This may mean that the various fractions of plankton nitrogen are not equally susceptible to bacterial attack.

Liberation of ammonia from plankton and other nitrogenous organic matter is, bacteriologically speaking, unspecialized, but is dependent upon the relative proportions of available nitrogen and carbon in the decomposing materials—the materials used in these experiments are, as Redfield (1934) has shown, characteristically nitrogen-rich.

Following the first burst of bacterial activity the ammonia concentration reaches a high level capable of supporting an active nitrite-forming population. Unsuccessful attempts were made to follow the development of the specific bacterial flora responsible for the oxidation of ammonia to nitrite. It appears from the many investigations upon nitrite-forming bacteria in the sea, that the process is due to specific organisms of the *Nitrosomonas* group analogous to the specialized nitrite-forming flora of soils (Waksman, Hotchkiss and Carey, 1933; Carey and Waksman, 1934). The rate at which nitrites are developed here is roughly the same as that observed in cultural studies of the process. Crude cultures prepared by inoculating sea water containing ammonium salts with mud or sea water usually give positive tests for nitrite within ten days or two weeks (depending upon the quantity of inoculum), after which the complete oxidation of ammonia to nitrite proceeds rapidly.

The final stage in nitrogen regeneration progresses more slowly, as is evident from Figs. 1 and 2. Nitrate formation is also effected by a specific bacterial flora, in this case, *Nitrobacter,* an efficient population of which seems to develop at a lower rate than either the non-specific ammonifying or specialized nitrite-forming bacteria. In culture experiments where crude inocula of nitrate-forming bacteria are added to sea water containing nitrite as the only sources of nitrogen, the period of incubation necessary to demonstrate measurable quantities of nitrate ranges from 30 to 90 days. Richer inocula bring about more rapid nitrate formation (Waksman, Hotchkiss and Carey, 1933).

It has been assumed that the relatively late appearance of nitrate in cultures made up of raw sea water to which organic nitrogen in some form has been added is due to the toxic effect of ammonia on nitrate-forming bacteria—a condition that has been clearly demonstrated in experiments on soils. But this relation, if it exists in these experiments, is masked by the slow growth of nitrate-forming bacteria even under favorable conditions. Thus in Series I and II the phase of nitrate formation began promptly after the disappearance of ammonia; in Series IV, on the other hand, it did not begin until 15 days after the ammonia had disappeared.

The regeneration experiments described here certainly are not identical with natural conditions and may not be expected to parallel exactly the courses of the individual phases of nitrate formation in the sea. On

the other hand, they offer a clear picture of their relations. Further, they validate the conventional conception of the nitrogen cycle as derived from the various studies of the individual processes, by bringing them together in a single summary experiment.

Summary

In conclusion, this study has shown:

1. That it is possible to reproduce the complete cycle of nitrogen regeneration.

2. That the transformation of decomposing plankton (especially diatoms) into ammonia is very rapid, beginning as soon as the initial substance disappears from the body. The amounts of soluble nitrogenous substances of higher molecular weight in these experiments can have been only very small.

3. The main stages in the decomposition are: dead body—ammonia —nitrite—nitrate.

4. Under these conditions, at least, no toxic substances are formed which inhibit the flowering of diatoms. The rapid and abundant development of the latter showed the regeneration of the water to be complete.

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Contribution No. 130

JOURNAL OF SEDIMENTARY PETROLOGY, VOL. 7, NO. 2, PP. 55–66, FIG. 1, TABLES 1–4.
AUGUST, 1937

BOTTOM DEPOSITS OF THE ROSS SEA

H. C. STETSON AND J. E. UPSON
Harvard University

Contribution No. 130 of the Woods Hole Oceanographic Institution

ABSTRACT

The Ross Sea is floored with glacial debris upon which the sea has exercised no selective action whatsoever. The sediment is apparently being laid down in the same condition in which it is being released by the melting ice. Distance from the ice barrier and depth of water have no effect on texture. The Antarctic continent is surrounded by a zone of this material 200 to 500 miles wide, which mantles the continental shelf and slopes. It might be termed a marine till. The percentages of clay and colloid run unusually high. Such complete lack of sorting is unusual in either a deep or shallow water marine sediment, even in the Arctic where the deposits are also largely laid down by floating ice.

Among the heavy minerals, those of the ferro-magnesian group are unusually abundant. All the heavies are comparatively unaltered, which is undoubtedly due to glacial conditions. Higher grade metamorphic minerals are notably absent. In the finer grades chemically decomposed material is found which is probably due to the glacial grinding of shales rather than to present conditions either on land or in the sea.

This paper presents the data of the mechanical and mineralogical composition of twelve cores obtained on the "Bear" by Edward Roos during the course of the second Byrd Antarctic Expedition. They are all located within the Ross Sea and the great majority along the front of the ice barrier (fig. 1). Although the cores are widely separated, the study seemed worth while because of the small number of bottom samples which have been obtained from this area, and because in its deposits we are dealing with a rather unusual type of marine sediment; one which has been laid down directly from a continental ice sheet with little or no modification. In the section dealing with the mineralogy, the data is insufficient to warrant more than a purely descriptive and qualitative report.

Our thanks are due to Professor Esper S. Larsen for much valuable criticism concerning the mineralogical examination.

MECHANICAL ANALYSIS

The method used for mechanical analysis was the combined sieve and hydrometer technique devised by Professor Arthur Casagrande. Before analysis the salt content of the sediment was removed by repeated washings, the water being drawn off through Pasteur-Chamberland filters by means of a vacuum pump. An account of this procedure is given elsewhere and further description is unnecessary here (1).

An attempt was made to use the statistical constants devised by Trask (2) for sorting and skewness, which are based on the relationships of the first and third quartile diam-

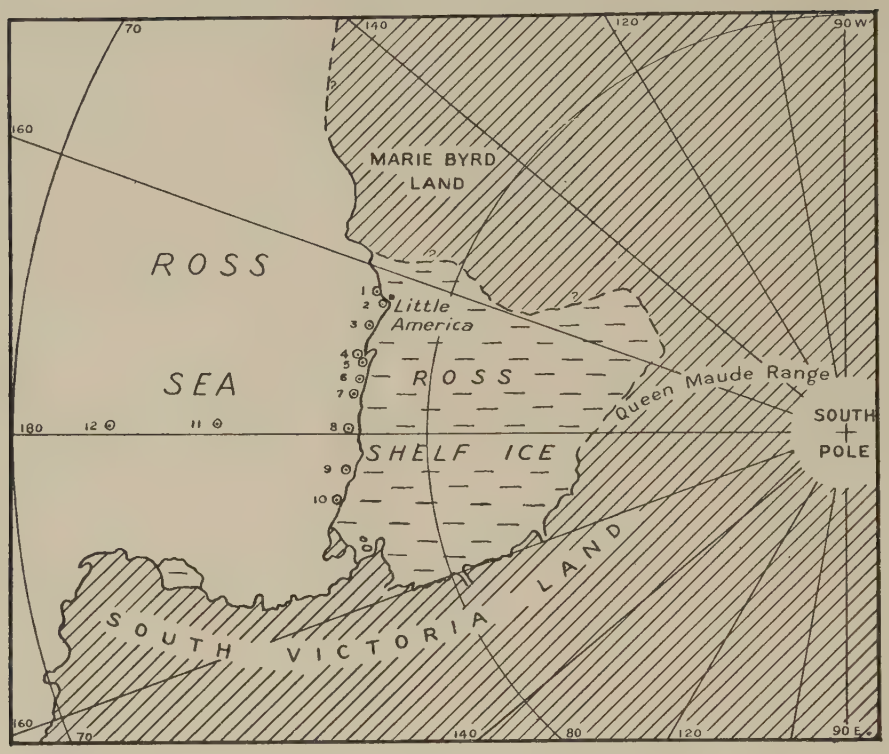

FIG. 1.—Positions of bottom coves.

TABLE I

Stations	Lat.	Long.	Depth, M.
1	78°–30′	S. 163°–40′ W.	642
2	78°–32′	164°–06′ W.	644
3	78°–20′	167°–17′ W.	530
4	78°–17′	170°–44′ W.	558
5	78°–20′	171°–37′ W.	539
6	78°–19′	173°–09′ W.	446
7	78°–16′	175°–37′ W.	545
8	78°–11′	179°–42′ W.	807
9	78°–00′	176°–35′ E.	803
10	77°–37′	172°–45′ E.	794
11	74°–57′	178°–45′ W.	520
12	72°–27′	178°–37′ W.	2571

eters to each other and to the median diameter. These quartiles are derived from a cumulative curve—75 per cent of the sample is finer than the diameter of the first quartile and 25 per cent finer than the third. It is generally agreed that it is not practicable to carry the mechanical analysis of a sediment further than one micron. Beyond this point the particles in suspension are so small that Brownian movement begins seriously to interfere with settling velocities. Consequently all calculations for grade sizes, based on Stokes Law, are subject to considerable error. In 16 out of the 24 samples analyzed, the portion of the sample smaller than one micron is more than 25 per cent of the entire sample; 40 per cent and more is common, and in one case it runs as high as 51 per cent. In many cases, therefore, it is impossible

to derive the third quartile diameter without extending the curves beyond the limits of accuracy.

The coefficient of sorting is obtained by substitution in the formula $So = \sqrt{\frac{Q1}{Q3}}$. Thus perfect sorting equals unity. The experience of the present authors with many samples has given an average value of 1.25 for beach sands, and of 1.45 for well-sorted, near-shore, sediments.

The coefficient of skewness is derived from the formula $Sk = \frac{Q1 \times Q3}{M^2}$. It indicates on which side of the median diameter, and how far from it, the mode, or peak of size distribution lies. For ease of interpretation, i.e., to show readily on which side of the median the mode lies and its relative divergence, the logarithm of the skewness is given. Thus a log of 0.0 ($Sk = 1$) indicates a symmetrical size distribution curve, the mode coinciding with the median; a plus log (Sk greater than 1) that the mode is on the fine side of the median; a minus the opposite. For full details Trask's papers should be consulted.

PREVIOUS INVESTIGATIONS

Our knowledge of the bottom deposits surrounding the Antarctic continent is mainly derived from the voyages of seven vessels—"Challenger" (3), "Valdivia" (4), "Gauss" (5), "Scotia" (6), "Aurora" (7), and of recent years "Discovery" and "William Scoresby" (8). Most of them ran lines of soundings across the southern oceans to Antarctica. "Challenger" approached what is now Kaiser William II Land and Termination Ice Tongue and thence proceeded to Melbourne. "Gauss" followed nearly the same route as "Challenger's" south bound track, going south and returning via Kerguelen. "Valdivia's" track lay somewhat to the west, from Bouvet Island to Enderby Land thence north to Kerguelen. "Scotia" crossed from the Falkland Islands to the Weddell Sea and thence northwards approximately along 10 W. Long. "Aurora" made several trips back and forth between Hobart and Adelie Land usually via Macquarie Island. "Discovery" and "William Scoresby" have sampled mostly in and around the Antarctic Archipelago, between these islands and Cape Horn, around south Georgia and in the Bellingshausen Sea.

It is evident from the above resume that the bottom deposits of the southern oceans are known, at least in a general way, from 160 W. Long. westward to about 90 E. Long. The remaining gap has been partly filled by the Ross Sea samples obtained by the "Bear."

DISTRIBUTION OF SEDIMENTS

Our knowledge can by no means be considered detailed, and it is of course impossible to delimit accurately the boundaries between the various types of deposits. Enough data, however, have been assembled to give an idea of their general distribution.

Antarctica is surrounded concentrically by three types of sediments.

Immediately encircling the continental margin is a zone of terrigenous material. This was originally put in the "blue mud" group according to Challenger Reports, but subsequent work has shown that it possesses very different characteristics from the terrigenous sediment commonly found in deep ocean basins. Philippi (5) and Pirie (6) have termed it a glacial marine deposit.

According to them it differs from "blue mud" in its very poor sorting, having a wide range in the size of its constituent particles, in its almost complete lack of $CaCO_3$, and low organic content. The "fine washings" consist largely of "rock flour" and the remainder of clay minerals. The samples consisted "essentially of a mixture of the finest ooze with sandy and gravelly constituents and here and there large fragments and stones." Chapman (7) is obviously dealing with the same type of material in his near-shore samples, though his descriptions are not so full.

Lying to the north of the glacial marine deposits is the zone of diatom ooze. Neaverson (8) has called attention to the intergradation of the deep sea deposits with one another, and the consequent difficulties of classification. Here the contact between the two zones was sampled in greater detail than was done by the other ships in their areas, and the terrigenous material was found to grade gradually into the organic ooze, with no sharp contact. Were comparable data available, it is probable that this condition would be found to exist all around the continent, and we would not find the clear cut boundaries that Philippi and Pirie imply. The width of the terrigenous zone is likewise variable, but in general it appears to extend 200 to 500 miles from the continental margins. Beyond the diatomaceous ooze lies the globigerina ooze characteristic of the deeper parts of all the southern oceans.

DESCRIPTIVE DATA

The Ross Sea lies entirely within the inner zone of glacial marine deposits, as the samples under consideration indicate. Table II lists the median diameters of the size distribution of each sample. Table III gives the percentage composition of each sample split up into arbitrary grade sizes, which are also taken from the cumulative curves. A table of this sort has all the disadvantages of a histogram, but if the faults are borne in mind, it is useful for a general survey. A section 5 to 7 cm. in length was taken from the top and bottom of each core, and in the case of core 12 one from the middle as well. The coring tube used had an inside diameter of about 1 inch, which necessarily limits the maximum size of the particles. Much larger rock fragments were obtained with another type of dredge. As most of the fine fractions were washed out when using this instrument, the samples were not analyzed.

Samples 1 to 10 were taken directly along the front of the ice barrier for a distance of nearly 300 miles. Their depths range from 446 to 807 meters.

TABLE II. *Statistical Constants*

Core	Length in cms.	Q1	Millimeters Median	Q3	So	Log Sk
1	32					
Sec. 1			0.0009			
Sec. 2			0.0012			
2	37.5					
Sec. 1			Flocculated			
Sec. 2			0.0029			
3	32					
Sec. 1			0.0032			
Sec. 2			0.0013			
4	35					
Sec. 1			0.0014			
Sec. 2			0.0017			
5	38					
Sec. 1			0.0017			
Sec. 2			0.0012			
6	30					
Sec. 1			0.0050			
Sec. 2		0.2250	0.0290	0.0010	15.0	−0.55
7	33					
Sec. 1		0.4900	0.0250	0.0009	23.2	−0.15
Sec. 2		0.4150	0.0820	0.0019	14.8	−0.93
8	30					
Sec. 1			0.0015			
Sec. 2		0.1620	0.0190	0.0019	9.2	−0.07
9	34					
Sec. 1			0.0031			
Sec. 2		0.2200	0.0210	0.0016	11.7	−0.10
10	36					
Sec. 1			0.0014			
Sec. 2			0.0016			
11	28.5					
Sec. 1		0.8100	0.1600	0.0260	5.5	−0.08
Sec. 2		0.1700	0.0140	0.0010	13.1	−0.06
12	53					
Sec. 1			0.0039			
Sec. 2		0.1020	0.0360	0.0021	6.9	−0.78
Sec. 3			0.0051			

The median diameters are all small, never exceeding 0.08 mm., and with the majority in the neighborhood of 0.001 mm. A marine sediment with a value for So. of 1.45 is considered well sorted, and values of 3 or 4 are not often exceeded. Consequently values ranging from 6.9 to 23.2 indicate that the sorting is very poor. In fact, some of the samples can scarcely be said to be sorted at all, so nearly equal is the proportion of material

TABLE III. *Percentage Composition*

Sample		Gravel 1–30 mm.	Sand 0.05–1 mm.	Silt 0.005–0.05 mm.	Clay 0.001–0.005 mm.	Colloid 0–0.001 mm.
Core 1	Sec. 1	4	6	14	25	51
	Sec. 2	9	7	13	24	47
Core 2	Sec. 2	1	28	14	13	44
Core 3	Sec. 1	16	9	19	21	35
	Sec. 2	0	8	23	21	48
Core 4	Sec. 1	0	6	24	25	45
	Sec. 2	2	8	25	22	43
Core 5	Sec. 1	1	9	24	24	42
	Sec. 2	1	11	17	24	47
Core 6	Sec. 1	4	23	23	18	32
	Sec. 2	11	34	18	12	25
Core 7	Sec. 1	20	27	16	11	26
	Sec. 2	14	40	15	11	20
Core 8	Sec. 1	2	13	18	23	44
	Sec. 2	13	26	26	15	20
Core 9	Sec. 1	5	18	20	21	36
	Sec. 2	9	34	22	15	20
Core 10	Sec. 1	0	8	23	26	43
	Sec. 2	0	7	21	31	41
Core 11	Sec. 1	23	49	13	10	5
	Sec. 2	10	30	18	17	25
Core 12	Sec. 1	0	20	26	19	35
	Sec. 2	4	41	35	6	21
	Sec. 3	0	21	30	16	33

in the different grades. The percentage of colloid runs unusually high, as does that of gravel. The combination of the two is responsible for the poor sorting. Core 11 is situated on the shelf about 210 miles seaward from the barrier. It displays the same characteristics as those just beyond the ice front. Core 12 was taken beyond the continental margin in 2571 meters of water. In spite of the depth of water, the material is very similar to that covering the shallower bottoms. The median diameters are no smaller, and the same lack of sorting due to the same causes, is present. Distance from the present ice front, and the depth of the water have no effect, per se, on texture.

The textural difference between the tops and the bottoms of the cores have no apparent significance. The same small median diameters and the same lack of sorting hold throughout. There is no tendency for any particular grade size to be dominant in either the top or the bottom. Environmental conditions under which

the lower parts of these short cores were deposited were, therefore, similar to those controlling deposition at present.

Pirie (6, pp. 683–684) states that the percentage of grade sizes larger than 0.02 to 0.05 mm. in diameter averages 16.7 per cent of the whole sample; and that the "fine washings," including everything below these limits, averages 82 per cent. He also emphasizes the fact that "rock flour" constitutes the bulk of these grade sizes by comparing them to clay from the Portobello brick field near Edinburgh, from which he says they are microscopically indistinguishable.

A precise definition of rock flour is needed. Pirie apparently uses this term to signify material which is composed almost entirely of fresh, sharply-angular mineral or rock fragments. It should be pointed out here that glacial gouge, or rock flour, of the above description can only be obtained by the scouring of crystalline rock surfaces. Rock flour derived from a shale would probably contain a large proportion of kaolin or other clay-like constituents. Pirie's methods of determination could not have been so critical as those of today.

In order to determine the relative amounts of "clay" and "rock flour" in the sediments from the Ross Sea, samples of cores 2, 5, 8, 10, and 12 were studied with a high-power oil immersion lense. No mineral separations were conducted, and the finest sizes of material could be studied, whereas in examining the heavy minerals, only the sand sizes were considered. The cores chosen are well-distributed over the area of the Ross Sea floor, and are taken to be representative of the whole. The relative amounts of the different constituents were estimated.

The proportion of fragments of diatoms and other organisms is high, amounting to as much as 50 per cent in some samples. There is a fairly high percentage of coarse mineral fragments, most of which are angular or subangular, although some are definitely rounded. There is an appreciable number of tiny grains so small as to be barely determinable as mineral particles. Many of these are muscovite or sericite, minerals which are often the result of alteration. Some of the feldspar grains are partly sericitized.

In addition there are many masses of tiny mineral fragments held together apparently by a matrix of clay-like material. The proportion of these rounded masses is in some samples as high as 25 per cent. This figure should not be taken as giving the actual percentage of "clay," since "clay" constitutes only part of these masses. The total proportion of angular mineral fragments is in every sample somewhat less than 50 per cent. If the organic material be ignored, however, this figure would be considerably higher. It is indicated, then, that at least 50 per cent of the rock debris studied might be considered "rock flour." However, the presence of some rounded grains, sericite, and the amorphous masses of tiny grains indicates that an appreciable, though not a major, part

of the Ross Sea material is the product of weathering. This may be explained by the glacial erosion of sedimentary and metamorphic rocks which may contain decomposition and alteration products. Glacial debris need not consist entirely of fresh angular particles.

HEAVY MINERAL CONTENT

Only the material of sand grade and larger was examined. The sands were subdivided by screening into four sizes: (1) greater than 1 mm. in diameter, (2) less than 1 mm. and retained by a 64 mesh screen, (3) passed by the 64 mesh screen and retained by a 130 mesh screen, and (4) that passing a 130 mesh screen. The heavy minerals were isolated by the use of bromoform, specific gravity 2.89. The material of the first two screen sizes contained many unbroken and undecomposed rock fragments, though the mineral content was qualitatively the same as that of the finer sizes. Consequently only the finer fractions were separated into heavy and light components; and the percentage of heavy minerals by weight was measured only for those sizes. The minerals were identified by optical methods.

The relative abundance of the different heavy minerals was estimated and the minerals classed as indicated in the accompanying table. No differences were observed between the top and bottom of any one core. Each is consequently treated as a unit in the table. Core 2, Section 1, had so little material in the sand grade that it was not analyzed.

The material of gravity less than 2.89 contains almost entirely quartz and feldspar (orthoclase and some plagioclase), with a little muscovite (partly sericite), and numerous rock fragments. The fragments consist of granite (both pink and gray), lava (probably basalt or andesite), felsite, biotite schist, some quartzite, pebbles of gray sandstone, arkosic sandstone or fine grained conglomerate, slate, and some fragments of serpentine. The igneous rocks are by far the most abundant.

In addition to this material which was in the cores, some pebbles and boulders brought up by dredge from the Bay of Whales were examined megascopically. These were similar to the fragments in the cores. Curiously enough, undoubted glacial striations were visible on only one fragment, a slate.

As indicated in Table IV the percentage of heavy minerals varies from 2 to 8. In nearly every core, the finer size contained a higher percentage than the next coarser grade. In general, all the material is fresh. However, the pyroxene and hornblende were slightly weathered in some of the cores. In the light fraction a few of the feldspars show some alteration. Nearly all the grains are angular, though some of the zircon and quartz grains, probably derived from the sediments, are rounded. No difference was observed, either in mineral content or in degree of alteration, between the top and bottom of any one core. This suggests the absence of weathering on the sea floor, though the cores are only about

TABLE IV

Core	1	2	3	4	5	6	7	8	9	11	12
Heavies in grade 3:	6%		3%	5%	2%	4%	4%	3%	5%	6%	5%
grade 4:	6%		6%	4%	4%	6%	7%	3%	8%	7%	6%
Minerals											
Pyroxene	C	D	R	C	A	A	A	C	A	D	A
Hornblende	A	C	A	A	—	C	C	C	C	C	C
Biotite	A	R	C	A	C	—	C	A	C	C	C
Epidote	C	C	C	R	R	R	A	C	C	C	R
Opaques	C	C	C	C	C	C	C	R	C	R	C
Garnet	R	R	R	R	R	R	R	R	R	R	R
Kyanite	R	R	R	R	R	R	R	R	R	R	R
Sphene	—	R	R	R	R	R	R	R	R	R	R
Zircon	R	R	R	R	R	R	R	R	R	R	R
Calcite	T	R	T	T	—	—	—	T	T	—	R
Tourmaline	—	T	T	T	T	T	T	T	—	—	T
Chlorite	R	T	R	—	T	R	T	—	—	—	—
Olivine	R	T	—	—	—	—	T	T	T	T	—
Clinozoisite	R	—	C	—	—	—	T	T	T	R	R
Rutile	—	—	T	T	T	T	—	—	—	T	—
Zoisite	—	R	R	C	R	—	—	—	—	R	R
Apatite	—	T	T	T	T	—	T	—	—	—	—
Chloritoid	—	T	T	—	—	—	—	—	T	—	—

NOTE: In addition to the above, a few grains of vesuvianite, topaz, and chiastolite were identified. Most of the pyroxene is augite, though some hypersthene is present in most of the cores. The letters indicate the following percentages: "D": more than 50 per cent of total, "A": 50 per cent to 20 cent, "C": 20 per cent to 5 per cent, "R": 5 per cent to 1 per cent, "T": 1 per cent or less.

$1\frac{1}{2}$ feet long. The only difference between cores is a rather pronounced decrease in the relative abundance of pyroxene in cores 1, 3, 4, as indicated in the table; and a less noticeable decrease in cores 5 and 6. The difference was apparent to the observer, but too small to be expressed by the percentage subdivisions used. Epidote is conspicuously rare in cores 4, 5, 6 and 12. In general, there is an accompanying increase in the amount of hornblende and biotite. All these cores were taken (with the exception of 11 and 12) off the edge of the Ross Sea Ice barrier. This may indicate a different source terrain for the sediments of that area.

CONCLUSIONS

The type of sediment which surrounds Antarctica is, as far as is known at present, unique among marine deposits. It mantles the continental shelf and slope, in general, down to about 2,000 fathoms. Pirie reports it as deep as 2,764 fathoms in one instance. The older techniques of mechanical analysis were inadequate for separating a sample into its constituent parts. Hence the data from these samples are not as complete as those which can be obtained by present day methods. Nevertheless, from the descriptions in the older reports, it is obvious that the zone of terrigenous material which the various vessels crossed in approaching the continent is the same type of deposit which floors the Ross Sea.

The continental ice sheet is responsible for this deposit, which has has all the characteristics of a till

laid down on land. The remarkable fact is how little influence the sea appears to have had upon it. Such a complete lack of sorting is unusual for marine deposits. Furthermore, the material deposited directly in front of the ice barrier is the same as that laid down 300 miles seaward. This uniform distribution is apparently characteristic of the whole width of this belt of sediment which surrounds the continent, as nearly as can be ascertained from the older analyses of samples taken in other parts of the area. The heterogeneous mixture of coarse and fine particles would indicate that deposition from melting icebergs is constantly taking place throughout the whole region. Marine currents have had little or no sorting effect upon the sediment, either while it was settling out or after its deposition. Nor do distance from shore or depth of water have any appreciable influence on texture, although were more samples available it would probably be found that there was some diminution in the median diameter towards the outer margins of this belt. In fact, Pirie states that his samples from the northerly parts of the Weddell Sea contain more amorphous clay than any of the others. The depth of water places these sediments well beyond the reach of wave action, so that once on the bottom the deposit apparently remains unaltered.

The major characteristics of the minerals are the freshness and angularity of the grains, the relative abundance of the heavy minerals as a whole, and the ferro-magnesian group in particular. The marked absence of higher-grade metamorphic minerals such as staurolite and sillimanite is worthy of record. This suite of minerals is the product of the two factors: constituents of the eroded rocks, and the manner of weathering and transportation. No minerals were identified which could not have been derived from the observed types of rocks. They are the same as those reported by Gould (9) from the Queen Maude Mountains. The mineral suite agrees well with Stewart's (10) petrographic description of specimens of the biotite schist collected by Gould. Exposure of considerable areas of basaltic rocks is suggested by the large proportion of pyroxene and other dark minerals. Gould observed diabase intrusives in some areas. The freshness and angularity of the material, and the great quantity of the more easily decomposed ferro-magnesian minerals, is explained by the presence of ice as the agent of transportation, and the presumed dominance of mechanical weathering.

The percentage of clay and especially colloid in these deposits runs unusually high, due to the failure of marine currents to elutriate the finer particles. By way of comparison, Thorp (11) gives the figures for the mechanical analyses of several samples in deeper parts of the Atlantic, as does Trask (2) for various localities all over the world. Rarely do the percentages for these two grade sizes reach the figures that are generally found here. These grades are by no means entirely

composed of fresh angular fragments, but considerable quantities of chemically altered material are present. As pointed out above, the altered material is probably derived from pre-existing sedimentary rocks.

For the sake of comparison let us examine some sediments from two areas in the Arctic which in large measure likewise owe their origin to floating ice, namely Davis Strait and the Polar Basin itself.

Trask (12) has analyzed the sediments brought back by the "Marion" Expedition from the Davis Strait region. In addition to the usual methods for transporting and distributing marine sediments, bergs of glacial ice and floes of sea ice, which pick up material from the shore line, also play an important part.

This material is much sandier than the Antarctic sediments which we have been considering, which is, of course, reflected in correspondingly larger values for the median diameter. The sorting, however, except for an occasional sample, is much better. It is evident that here marine currents are exerting some selective action on the heterogeneous mass of glacial debris which is being constantly delivered to them. This sorting may take place while the material is settling from the surface, or the bottom itself may be swept by currents of sufficient velocity to remove the finer grades.

In the Arctic Basin proper (1) we have yet another type of deposit, resulting from floating ice. Like the Antarctic deposits, it contains unusually large amounts of clay and colloid for a marine sediment, with equally small median diameters, but the sorting is good. It does not possess the usual characteristics of a deep-water marine clay, but more nearly resembles a fluviatile one. Its mode of origin is utterly different from the material being deposited in the oceans at the other pole. The ice of the Arctic Basin is all salt-water ice. There are no bergs present which originated in glaciers. During the winter an ice platform forms over the broad Siberian continental shelf, with its inner margin frozen solidly to the land. The spring freshets of the Siberian rivers start in the south while this ice is still fast to the shore. In the consequent flooding of the surface of the ice-floes much river sediment is carried out upon them. Eventually, as the spring advances, these floes break loose and drift away with their load of sediment to join the main polar ice-pack. There is ample opportunity for this material to be dropped during the extensive melting of the summer. It is probable that the ordinary marine agencies supply some of the material for this deep water clay, but the direct deposition of river sediment by the ice plays a larger part.

The marine sediments at the two poles exhibit great diversity. The fact that neither region has emerged from the Ice Age does not make for uniformity of conditions of sedimentation, which at first glance one might be led to expect. Were these

sediments ever to be consolidated and form part of the geologic column, from the Davis Strait region, and in all probability off the whole west coast of Greenland, we should have a poorly-sorted marine sandstone, still retaining traces of its glacial origin; in the Arctic Basin would be very fine-grained shales giving no textural indication that they had ever been associated with ice or an Arctic climate; while on the continental shelf and slopes of Antarctica one should find a vast deposit of tillite. Sedimentary environments, under an Arctic climate, it appears, may be just as varied as under more temperate conditions.

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Contribution No. 131

INTEGUMENTARY COLOR CHANGES OF ELASMOBRANCH FISHES ESPECIALLY OF MUSTELUS

G. H. PARKER

(*Read November 27, 1936*)

Abstract

Squalus acanthias is a dark dogfish that shows little or no evidence of a pale phase. As it blanches somewhat on loss of its pituitary gland its general darkness indicates a certain continuity of pituitary secretion independent of its environment. *Mustelus canis* and *Raja erinacea* show well marked dark and pale phases in response to changes in their surroundings.

The dark phase in these three elasmobranchs is due to a neurohumor from the intermediate lobe of the pituitary gland carried in the blood from the gland to the melanophores, a hydrohumor. This substance, contained in commercial pituitrin and in intermedin, is different from the oxytocic and the pressor principles from the pituitary gland.

The pale phase in these fishes is due to the absence from the blood of any dispersing factor (*Raja erinacea*), or to the action of nerves (*Mustelus canis* and *Squalus acanthias* in part). In these three elasmobranchs there is no evidence of a W-substance such as has been found in *Scyllium* and in some species of *Raja* by Hogben.

The pinkness of pale elasmobranchs may be as much due to the exposure of the dermal blood-vessel by pigment concentration as to the absence of a pressor factor. The color changes in elasmobranchs are slow in accomplishment involving hours and days, a condition associated with their usual means of excitation, chiefly hydrohumors.

Adrenalin blanches *Mustelus canis*, *Squalus acanthias*, and *Raja erinacea* but probably plays no part in the natural paling of these fishes. The concentrating neurohumor in such elasmobranchs as *Mustelus* and *Squalus* is not carried by the blood; it is a lipohumor. It is soluble in olive oil, ether, but not in water. It resists heat to 110° C., the action of sodium hydroxide and of hydrochloric acid. It is a relatively stable compound, possibly a sterol.

1. Introduction

In teleost fishes the integumentary color changes have been matters of interest since the earliest times, but in elasmobranchs these changes have received attention only during the last decade and a half. Brief as this period is it has been long enough to show that the color changes in cartilaginous fishes are in many respects like those in other animals particularly in that they are brought about in different species by means often strikingly diverse and even unique. According to various investigators animals with active

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chromatophores, particularly melanophores, may become normally dark in several ways: through the direct action of light on the skins of enucleated forms including fishes (Pouchet, 1871), through the action of the neurohumor carried in the blood from the intermediate lobe of the pituitary gland, as in almost all chromatic vertebrates (Hogben, 1924); through the lipohumors from the dispersing nerve-fibers of certain fishes, such as *Fundulus* and *Ameiurus* (Parker, 1933a, 1934b), and probably through other means still to be discovered. They may become pale in some half a dozen different ways: through the direct effect of darkness upon the skin of blinded animals as salamander larvæ (Babák, 1910) and fishes (von Frisch, 1911); through the action of adrenalin transported by the blood, as in Phrynosoma (Redfield, 1918); through the mere absence from the animal's blood of a dispersing agent such as the pituitary neurohumor as was originally claimed for amphibians (Hogben and Winton, 1922); through the neurohumor from the *pars tuberalis* of the pituitary complex, as in certain toads and frogs (Hogben and Slome, 1931); and through the lipohumors from the concentrating nerve-fibers of *Fundulus* and other fishes (Parker, 1934a). When one keeps in mind that this catalogue of the means of melanophore change is assuredly incomplete and that any given species may employ not only one or other of these means but combinations of them, the room for diversity in the mechanisms controlling color responses must be admitted to be considerable. As the following discussion will show, more or less of this diversity is realized in even so compact a group of vertebrates as the elasmobranchs where, so far as our present information goes, scarcely any two species employ identical means for color change.

The fishes upon which the following studies were based are the smooth dogfish, *Mustelus canis*, the spiny dogfish, *Squalus acanthias*, and the skate, *Raja erinacea*, all from the region about Woods Hole. The work was done in part at the Oceanographic Institution and in part at the Marine Biological Laboratory both at Woods Hole. To the Directors

of these two institutions and to their very efficient corps of assistants I wish to extend my sincere thanks. The special expenses of the research were met by a generous grant from the Milton Fund of Harvard University to whose administrative officers I am under great obligation.

2. Technique

The only special feature in the technique of the problem that calls for comment was the use of cold as a stupefying agent in place of drugs. The profound and somewhat lasting effect of the common anesthetics such as ether, urethane and the like on chromatophores led me to stupefy by means of cold. It was found very convenient to immerse fishes in a mixture of cracked ice and seawater for stupefaction. After a quarter of an hour or so in such a mixture the fish was found to have become fully passive and on removal from the cold it remained in this condition for ten to fifteen minutes during which an operation could be easily carried out. All the operations were of a relatively simple character and were usually completed in at most ten minutes. After the operation the fish was placed in an aquarium of seawater where it recovered quickly, for there was no drug to be eliminated. The advantage of this method of stupefaction over those in which drugs are used is obvious. The ice mixture was put in any small vessel for small fishes and in a barrel or tub for large ones. This method ought to find easy application for the stupefaction of any cold-blooded animal.

3. Normal Color Responses

A number of elasmobranchs appear to be almost if not quite devoid of color responses to such surrounding changes as would call forth active alterations of tint in many other fishes. *Raja clavata* and *R. batis*, both described as darkish species, are said by Schaefer (1921) not to change in color at all on being transferred from a black to a white background. *Squalus acanthias*, a dark dogfish, when introduced into an illuminated aquarium with white walls, will ordinarily show

no change of tint though some individuals under such circumstances will in the course of two days blanch slightly. These moderately pale fishes on being transferred to a tank with black walls will slowly reassume their original dark color. After the complete removal of the pituitary gland from any dark *Squalus* the fish will blanch slowly even in a tank with black walls (Parker, 1936a). This observation has been confirmed by Hogben (1936) on *Raja clavata* which though a normally dark inactive species, as originally noted by Schaefer, will also blanch on the loss of its pituitary gland. Both *Scyllium catulus* and *S. canicula* appear to be relatively inactive in their color changes (Young, 1933; Hogben, 1936; Wykes, 1936). Like *Squalus acanthias* and *Raja clavata* they also blanch somewhat on the loss of their pituitary glands. Notwithstanding the fact that all these relatively inactive, dark forms show very little or no color response to changes in their environment, their dark color can not be attributed to a complete lack of ability to change their tint, for on the loss of their pituitary glands they blanch noticeably. Their more or less constant dark coloration is therefore probably due to a steady production of a dispersing pituitary neurohumor, a production which is apparently not influenced to any considerable extent by environmental changes.

In contrast with these inactive elasmobranchs may be placed a number of active species of which the color responses to environmental differences are pronounced and unquestionable. *Mustelus canis*, of which extreme differences in tint were first noted by Lundstrom and Bard (1932) in their experiments on the pituitary gland in this fish, is dark on a black background and very pale on a white one (Parker and Porter, 1934). Adult fishes change from the pale to the dark phase in from half an hour to two hours. The reverse change from dark to pale requires some two days. The two phases in *Mustelus* are so strikingly associated with the environmental conditions that it is strange that Hogben (1936) could have had any doubt on this matter. The pups of *Mustelus canis* immediately after birth are fully responsive in their color

changes to the condition of their surroundings (Parker, 1936b). These young fishes change from pale to dark in less time than from dark to pale as is characteristic of the adults. Other elasmobranchs that show active color responses are *Raja erinacea* (Parker, 1933b), *R. brachyura*, *R. maculata*, and *Rhina squatina* (Hogben, 1936; Wykes, 1936). In all these forms the color changes are recorded as from the dorsal aspect of the fishes. In *Raja oxyrhyncha* Weidenreich (1927) has described a change of tint that takes place on the ventral surface of this species, a remarkable and somewhat puzzling phenomenon.

4. The Dark Phase

The dark phase of elasmobranchs so far as it has been studied appears to be excited exclusively by pituitary secretions. This was first made clear by Lundstrom and Bard (1932) in their study of *Mustelus*. When the pituitary gland is removed from this and other elasmobranchs the fishes invariably become pale, some more, others less (*Mustelus canis*, Lundstrom and Bard, 1932; *Squalus acanthias*, Parker, 1936a; *Scyllium canicula*, *S. catulus*, *Rhina squatina; Raja brachyura*, *R. clavata*, *R. maculata*, *R. microcelatus;* Hogben, 1936; Wykes, 1936; Waring, 1936a, 1936b). An injection of an extract from the pituitary gland into such pale elasmobranchs is always followed by a darkening of their integument. No other organ than this gland is known to be connected thus with the dark phase of these fishes. If the blood of a dark *Squalus* is injected into a slightly pale one, a dark spot is produced though such blood has no effect on a dark fish. Blood from a pale fish is without influence on either dark or pale individuals (Parker, 1936a). What is true of the blood of *Squalus* appears also to be true of that of *Mustelus* (Parker and Porter, 1934). These observations have convinced most investigators that the dark phase of elasmobranchs is excited by a neurohumor produced in the pituitary gland and carried thence by the blood to the responding melanophores.

It is generally assumed that the production of this neurohumor is controlled through the eyes of the fish and to a

considerable extent this is true. When the eyes of *Mustelus* are removed the fish will within a few hours assume a dark tint which is then maintained with more or less constancy irrespective of the surroundings. In some instances the coloration may be extreme in depth (Parker and Porter, 1934). In *Raja brachyura*, according to Hogben (1936), the eyeless fish takes on a tint between pale and dark. If from a blinded dark *Mustelus* the pituitary gland is removed, the fish soon becomes fully pale, showing that the dark phase of the blinded individual was still dependent upon the pituitary neurohumor. The exclusion of the eye from any direct control over this tint in the fish is seen from the fact that a hypophysectomized and consequently pale fish does not change its tone to any observable degree on being enucleated. The eyes are concerned with the control of the gland only from the standpoint of environmental changes exciting or inhibiting it in response to the state of the surroundings. A smooth dogfish whose optic nerves have been cut darkens in precisely the same way as one whose eyes have been removed. Such a condition shows that the control exerted by the eyes of this fish over its pituitary gland is not through a hormone given out by the retina or other such part, and carried by the blood to the pituitary gland, but by nerve impulses transmitted from the retina over the optic nerve to deeper parts.

The neurohumor produced by the pituitary gland and concerned with the dispersing of pigment in the elasmobranch melanophores has been shown to come from the posterior or neuro-intermediate lobe of the gland (*Mustelus*, Lundstrom and Bard, 1932; *Raja brachyura*, *R. maculata*, Hogben, 1936; *Scyllium canicula*, Waring, 1936a). Extracts from this part of the gland always act as darkening agents. The commercial pituitary products "pituitrin" (Parke, Davis and Co.) and "infundin" (Burroughs, Wellcome and Co.) both darken *Mustelus* (Lundstrom and Bard, 1932; Parker, 1935b) and the former has been shown to darken *Squalus* (Parker, 1936a). Through the kindness of Dr. F. L. Hisaw I was enabled to test samples of intermedin made in his laboratory by Dr. H.

L. Fevold.[1] Intermedin is a pituitary extract which by its method of production is freed from the oxytocic and vasopressor principles contained in ordinary pituitary extract. It is convenient to express the concentration of intermedin, as described in the accompanying note, on the basis of the amount of extract derived from one gram of dry gland and dissolved in one cubic centimeter of water. In the actual tests 0.5 cc. of solution at various dilutions was injected hypodermically into the sides of pups of smooth dogfishes. Each pup weighed about 100 g. and had a length of some 35 cm. The results of these injections are shown in table 1.

TABLE 1

Color responses of three sets of smooth dogfish pups (*Mustelus canis*) I, II, and III, into each of which 0.5 cc. of an aqueous solution of intermedin had been injected. The full strength solution of intermedin is assumed as that in which the extract from 1 g. of dry pituitary gland is contained in 1 cc. of water. The dilutions are expressed in the fractions of grams of dry gland substance that yielded the extract injected. The dogfishes in the beginning were pale and were kept in an illuminated aquarium with white walls.

Grams of Dry Gland as Source of Extract in 0.5 cc. Water	Integumentary Tints of the Three Sets of Dogfishes		
	I	II	III
0.2	Dark	Dark	Dark
0.1	Dark	Dark	Dark
0.05	Darkish	Darkish	Dark
0.025	Pale	Darkish	Pale
0.0125	Pale	Pale	Pale
0.00625	Pale	Pale	Pale
H_2O	Pale	Pale	Pale

As table 1 shows 0.5 cc. of intermedin solution may darken a smooth dogfish pup when the concentration of the solution

[1] The intermedin used in these experiments was prepared by Dr. H. L. Fevold from powdered, whole, pituitary glands of sheep. The solution of intermedin was an 80 per cent ethanol soluble fraction of an alkaline extract of the powdered gland. The ethanol was evaporated and the residue was dissolved in water so that each cubic centimeter of water contained the extract from 50 grams of the original pituitary powder. This was used as a stock solution and various dilutions as desired were made from it. Amounts of intermedin injected into dogfishes could therefore be expressed as equivalent to a given number of grams of the original powder. Thus a 0.2 gram solution was one in which each cubic centimeter of fluid contained an amount of extract that was obtained from 0.2 gram of the dry, powdered gland.

is such as is obtained from 0.025 g. of dry gland in 0.5 cc. of water. Weaker than this the solution is ineffective; stronger it is invariably effective. The dispersing neurohumor for elasmobranch melanophores must be contained in such extracts though it cannot be stated in how pure a form it exists. This neurohumor, the B substance of Hogben, must also be contained in commercial infundin and pituitrin but not in pitocin (Parke, Davis and Co.) which, though it is the carrier of the oxytocic principle, does not darken dogfishes (Lundstrom and Bard, 1932). I agree with Hogben (1936) in the belief that this neurohumor is not the same as the pressor substance contained in pitressin, for, though pitressin was found by Lunstrom and Bard to darken dogfishes, it did so, I suspect, not because of the pressor substance it contained but in consequence of a certain amount of true dispersing neurohumor included in the pitressin as an accidental impurity.

Excepting by means of the dispersing neurohumor of the intermediate lobe of the pituitary gland I know of no way of profoundly darkening the elasmobranch skin. This blood-soluble neurohumor appears to be the one and only agent thus directly concerned with the dark phase. In eyeless selachians, and in probably many other blinded animals, it seems to be continuously produced and the animals remain in consequence moderately dark. When the eyes are functional and the fishes are on an illuminated black background it is present in large amount; on a white background it may be entirely absent probably as a result of glandular inhibition excited through the eyes by the white surroundings. It must not be forgotten that eyeless *Mustelus* from which the pituitary gland has been removed are often still able to show a slight color change, darkening in bright light and blanching in darkness, reactions which are probably due to the direct effect of the light or its absence on the melanophores.

5. The Pale Phase

The blanching of elasmobranchs is a more intricate process than their darkening. It may be due to the mere absence of an agent active in dispersing pigment, as was implied by Lundstrom and Bard (1932). It may result from the action of concentrating nerves, as was advocated by Parker and Porter (1934). It may be occasioned by the presence of an active concentrating neurohumor, as has been maintained recently by Hogben (1936). Or it may be the outcome of factors still to be discovered. Among the various means that have been proposed thus far as the exciting agents in the blanching of these fishes no instance of mutually exclusive elements has occurred; hence in any given elasmobranch these suspected agents may be present singly or in any combination. In discussing the means by which elasmobranchs may blanch I shall begin with a consideration of a concentrating pituitary hormone.

Hogben's contention that elasmobranchs blanch as a result of a concentrating hormone called by him the W substance, which excites the pale phase in these fishes as the dispersing pituitary hormone excites the dark one is set forth in his most recent paper on this subject (1936). This view is an extension to elasmobranchs of conclusions originally arrived at by Hogben and Slome (1931) from their study of amphibians. The evidence advanced by Hogben in favor of this view as applied to sharks and rays is drawn from a study of *Scyllium canicula*, *S. catulus*, and *Raja brachyura*. Hogben believes that the W substance in these fishes is derived from the anterior pituitary lobe. When in a dark fish this lobe is removed no change in color is noted. If this lobe is removed from a pale fish, however, the creature becomes dark even though it is kept on a white background, an observation confirmed by Waring (1936a). Thus the loss of the anterior lobe abolishes temporarily and perhaps permanently the pale response. Implanting an anterior lobe into a pale fish produced negative or relatively slight results. Implanting such a lobe into a dark fish produced so slight a change as to

justify no definite conclusion. As Hogben remarks the inconclusiveness of much of this work is due in large measure to the difficulties in managing marine animals, a hindrance that is familiar to every one who has worked on selachians. From results almost identical with these Waring (1936a) was led to conclude that in *Scyllium* the anterior pituitary lobe, though not directly concerned with blanching, was the means of activating the immediate mechanism for this operation, a mechanism which according to this worker may be either humoral or nervous but which at present is quite obscure.

When the anterior pituitary lobe of *Mustelus* is removed, the fish will continue to change from pale to dark and the reverse in an entirely normal way. This dogfish, however, possesses concentrating nerve-fibers and hence these fibers may replace the possible activity of the anterior pituitary lobe. However the removal of the whole pituitary complex, as has long been known, will induce the fish to assume in a short time a maximum pallor even in a black-walled illuminated reservoir. This observation, first made by Lundstrom and Bard, has been repeated often by others and shows conclusively that the pituitary gland, including its anterior lobe, is not necessary for the complete blanching of this fish. It does not, however, allow the conclusion to be drawn that this gland may not play some part in this process. What is true of *Mustelus* is for the most part true of *Squalus* where concentrating nerve-fibers are few or in certain individuals probably entirely absent. A more conclusive instance, however, is seen in *Raja erinacea* where nerves have no part whatever in blanching. In this species the loss of the pituitary gland is followed by a maximum paling showing clearly that this operation may be fully completed in the absence of this gland.

If a concentrating pituitary neurohumor, such as the W substance of Hogben is believed to be, is present in selachians, it ought to be identifiable in the blood of these fishes when they are in the pale state. Tests to this end were carried out on the three common species at Woods Hole and have been

reported already in part. Such tests consisted in the transfer of a certain amount of blood from pale fishes to moderately dark ones on the assumption that the partly dispersed pigment in the melanophores of the recipients would thereby be concentrated. Of the score or more tests of this kind that have been carried out on *Mustelus canis* (Parker and Porter, 1934) and on *Squalus acanthias* (Parker, 1936a) none has ever given a positive result. In all instances the dogfishes into which the injections were made neither developed pale spots nor changed noticeably in tint.

Another set of tests which were directed particularly at this question were carried out in *Raja erinacea.* This skate has been shown quite clearly to have no nervous control over its melanophores. It nevertheless changes from pale to dark and the reverse in a very clear and unmistakable manner (Parker, 1933b). At three different times when this species was sufficiently abundant at Woods Hole tests were made in the following way. Two medium-sized skates were kept some two to three days in an illuminated tank with black walls till the fishes were fairly dark. At the same time a third skate was kept in an illuminated white-walled tank till it was completely pale. This pale fish was then fully bled from the caudal artery, the blood thus obtained was defibrinated, and 1 cc. of it was injected into a pectoral fin of one of the two dark skates, the other being held for comparison. Both dark skates, now together in the same black-walled, illuminated aquarium, were kept under close inspection over a period of some eight hours. At no time during this interval was the injected skate seen to develop a pale spot in the region of the injection nor to change its general tint. The other two tests, which were essentially like the one just described, also yielded no evidence in favor of a blanching hormone in the blood of the pale fish. The same technique when applied in a reciprocal way to the blood of a dark individual regularly yielded satisfactory evidence of a dispersing neurohumor, a result that indicates the reliability of the procedure. I therefore conclude that at least in *Raja*

erinacea the pale phase is not due to a concentrating pituitary neurohumor carried in the blood such as the W substance hypothesized by Hogben. Whether this conclusion will hold for other elasmobranchs than *Raja erinacea* and particularly for those forms from which both Hogben and Waring removed the anterior pituitary lobe and thus abolished blanching remains to be determined. Different species of fishes show in the details of their color control great diversity.

A second suggested way by which elasmobranchs may blanch is through the absence in their blood of any dispersing neurohumor. This implies that a melanophore when left to itself naturally drifts into a state with concentrated pigment, an assumption often met with but by no means established. This general explanation of blanching was adopted by Hogben (1924) in his early work on amphibians but was eventually discarded by him. As already noted it is implied but not precisely expressed by Lundstrom and Bard (1932) in their study of *Mustelus*. In this dogfish, as the work of Parker and Porter (1934) shows, the pale phase involves concentrating nerves and consequently it is difficult to say whether this second method of blanching can be said to apply or not to *Mustelus*. With *Raja erinacea* the case is quite different. This fish, as already pointed out, darkens in consequence of a dispersing pituitary neurohumor in its blood. It blanches in a clear and obvious way and yet it appears to have no concentrating nerves and its blood when transferred gives no evidence of containing a concentrating neurohumor. There seems to be little left to fall back upon as an explanation of how this fish assumes its pale phase except the supposition that the gradual disappearance of the dispersing substance from its blood allows its melanophores of themselves to concentrate their pigment. This assumption is not without a certain amount of support, for the same condition has appeared in certain American frogs recently studied in the Harvard Laboratories, a condition unlike that reported a short time ago by Hogben for South African and European amphibians. Whether or not this explanation of blanching holds for the

selachians studied by Wykes (1936) cannot be stated. In *Raja brachyura*, *R. maculata*, *Rhina squatina*, *Scyllium canicula* and *S. catulus*, there is good evidence according to this investigator for the conclusion that nerves play no part in color changes, but whether these fishes blanch in consequence of the presence of a concentrating neurohumor or of the absence of a dispersing one cannot be affirmed till such tests as, for instance, those involving transfers of blood have been tried.

Although the evidence here brought forward so far as the present problem is concerned must be admitted to be fragmentary and inconclusive for *Mustelus* and *Squalus* that for *Raja erinacea* is quite otherwise. The pale phase of this ray is due neither to direct nervous action nor to a concentrating neurohumor in its blood. It appears to result from the mere absence of a dispersing factor.

The third view as to the blanching of elasmobranchs is that this operation depends upon the direct action of concentrating nerves on the melanophores in these fishes. The evidence for this conclusion has already been presented in a series of papers (Parker and Porter, 1934; Parker, 1935a, 1935b, 1936a, 1936b, 1936c) dealing with *Mustelus*. When a cut is made into the substance of a moderately dark *Mustelus canis*, especially through a fin of this fish, so as to sever integumentary nerves there appears in the course of ten to fifteen minutes a pale splotch or band which extends from the region of the cut over the skin, for instance, to the edge of the fin. These light areas follow the distribution of the nerves, not that of the blood-vessels (Parker and Porter, 1934). They can be excited by electric stimulation as well as by cutting (Parker, 1935a). After they have faded they can be revived by a new cut (Parker, 1936c). They result from a concentration of pigment in the melanophores and the evidence thus far accumulated points conclusively to them as the result of the temporary activation of concentrating nerves. They are noticeable in pale dogfishes as well as in dark ones showing that their method of excitation is on

the whole more efficient than that by which the normal paling of this fish is elicited. They are as easily excited in the pups of *Mustelus* as in the adults (Parker, 1936b). Thus there appears to be perfectly good ground for the belief in the presence of concentrating nerve fibers in this dogfish and that these fibers are concerned with its pale phase.

That all elasmobranchs are not thus provided with fibers of this class seems also equally certain. As early as 1933 Young in his exhaustive paper on the autonomic nervous system of selachians pointed out that in *Scyllium* no change in color was observed after section of the spinal, trigeminal, or facial nerves. He was therefore led to conclude that there was no direct nervous control of the melanophores in this fish. These observations were in support of his findings that in the deep-seated autonomic connections in this and other selachians there were no gray rami communicantes, tracts over which the postganglionic nerve-fibers controlling color changes pass from the sympathetic ganglia to the spinal nerves and thence to the melanophores. So far as the absence of color changes due to the cutting of nerves is concerned Young's observations on *Scyllium* have been confirmed by Waring (1936a) as well as by Wykes (1936) who also has shown that nerve section in *Raja brachyura* and *R. maculata*, and nerve stimulation in *Raja brachyura*, *Rhina squatina* and *Scyllium catulus* fail to induce color changes. As already noted the section of pectoral nerves in the American *Raja erinacea* (Parker, 1936) is without effect on the color of this species. In *Squalus acanthias* on the other hand individuals differ; in some instances faint bands result from the section of nerves, in others not. Thus this species seems to hold a somewhat intermediate position between *Mustelus*, the blanching of which is nervous and a considerable number of other selachians, *Scyllium*, *Raja*, and *Rhina*, in which it is non-nervous. Whether in these three forms blanching is due to a pituitary neurohumor such as the W substance of Hogben or to the mere absence from the blood of a dispersing neurohumor cannot be stated with certainty though from what

has been presented concerning *Raja erinacea* it seems probable that the hypothesis of absence is the correct one.

6. Adrenalin

Adrenalin almost invariably induces pigment concentration in the vertebrate melanophores. It is therefore natural to suspect this hormone in any instances where concentration of pigment occurs and where other exciting agents have not been identified. Lundstrom and Bard (1932) were the first to point out that adrenalin blanched elasmobranchs. When 1 cc. of a 1 : 1000 solution of adrenalin hydrochloride was injected into a smooth dogfish the fish, according to these authors, began to pale in some ten minutes. This blanching reached a maximum in about an hour and persisted approximately two hours. The dose of adrenalin was admittedly enormous. This result was confirmed by Parker and Porter (1934) who found that 0.5 cc. of 1 : 10,000 would induce a temporary blanching in an adult smooth dogfish. *Mustelus* pups reacted to this hormone in much the same way as adults did (Parker, 1936b). Young (1933) was unable to induce pallor in *Scyllium canicula*, *S. catulus* and *Torpedo ocellata* by the injection of 1 mg. of adrenalin hydrochloride, though this dose was amply sufficient to blanch *Pleuronectes*. Wykes (1936) was able to produce only a small degree of pallor in *Raja brachyura* and *Rhina squatina* by injecting 1 cc. of a 1 : 10,000 adrenalin hydrochloride, a change which she is inclined to attribute to vaso-constrictor action. Possibly in Young's tests and certainly in those by Wykes the concentrations used were very close to the effective limits of this hormone judged from the data given for *Mustelus*. Here the effective doses were truly prodigious. In fact they were so large that it is incredible that this hormone, even though it does cause concentration of pigment in a number of elasmobranchs, can be a normal physiological agent in inducing such changes. That the blood of pale elasmobranchs, *Mustelus*, *Squalus*, and *Raja*, has no effect whatever on the melanophores of dark or partly dark individuals leads to the

conclusion that in those selachians tested adrenalin probably plays no part in their blanching (Waring, 1936a).

7. Pinkness of the Pale Phase

Almost all who have worked extensively on the color changes of elasmobranchs have been struck by the pinkness which often accompanies the pale phase. This was noticed in *Mustelus* by Lundstrom and Bard (1932) and by Parker and Porter (1934). It is also recorded by Hogben (1936) for certain skates from which he had removed the pituitary glands. Hogben following a suggestion by Krogh (1922) was inclined to attribute this pinkness to the absence of the pressor principle from the blood of the hypophysectomized fishes. Although this explanation may apply to a certain degree it must not be forgotten that elasmobranchs which have blanched normally also take on a pink hue. Thus if a *Mustelus* is put in a white-walled illuminated tank, it will become pale in the course of about two days toward the end of which period the pink tone gradually asserts itself. It is of course possible that during this time pressor substance may have gradually diminished in the blood and the blood-vessels in consequence may have become enlarged, but it is also true that by the concentration of melanophore pigment the integumentary vessels become more readily visible. Certainly the pink tint which is acquired as dogfishes blanch normally is due in part if not in whole to the mere exposure of the blood vessels irrespective of their change in calibre.

8. The Concentrating Neurohumor

The pale phase of *Mustelus* has already been shown to be due to the direct action of concentrating nerves on the melanophores of this fish (Parker and Porter, 1934). These nerves have been suspected of acting on the color cells through an oil-soluble substance discharged from their terminals, a suspicion that has been justified by the extraction of such a substance from the fins of pale *Mustelus* (Parker, 1935b). Olive oil extracts, cold ether and Soxhlet ether extracts of

pale fins of *Mustelus* when injected subcutaneously into a dark individual induce the concentration of its melanophore pigment. Injections of seawater, of pure olive oil, of olive-oil extracts of dark fins or of muscle, seawater extracts of pale fins, and defibrinated blood from pale or from dark fishes have no effect whatever on the integumentary color of this dogfish. In consequence of these observations the concentrating agent in *Mustelus* is believed to be an oil-soluble hormone, a lipohumor, of nervous origin.

To carry this inquiry toward a more quantitative stage efforts were made to standardize the effective extract. The fins of three adult smooth dogfishes that had been well blanched in the course of several days were cut off and dried over night in a chemical oven held at a temperature between 105° and 110° C. The weight of the dried fins was 72.4 g. These dry fins were then thoroughly pulverized and extracted in a Soxhlet apparatus with ether over a period of six hours. The Soxhlet waterbath had a temperature of about 65° C. and a turnover of once in about 20 minutes. The ether extract thus obtained was yellowish in color and after full evaporation left a thick, yellowish, oily residue which from the three sets of fins weighed 1.02 g. This residue was mixed with an equal volume of cold-blooded Ringer's solution and the mixture thus obtained was regarded as standard. From this standard mixture dilutions were made by adding appropriate amounts of pure Ringer's solution. Dilute mixtures prepared in this way were then tested by being injected hypodermically into the dorsal flank of a *Mustelus* pup (approximate length 35 cm., and weight 100 g.). The amount introduced into the pup was 0.05 cc. and the fish was subsequently watched for any color change. The results were comparatively simple. The standard mixture and that composed of one part of standard and one part of Ringer's solutions invariably produced pale spots on the skin of the fishes. Dilutions of one part of the standard mixture in ten, fifty, one-hundred, and one-thousand parts of Ringer's solution induced no color change at all. Plainly the standard mixture,

so-called, is not far from the limit of physiological efficiency. This result led me to repeat a test which I had previously carried out and which had yielded rather contradictory results. In table I of my former paper (Parker, 1935b) I entered the observation that an olive-oil extract from the pale skin of *Mustelus* had failed in the two dark fishes tested to induce local blanching. This observation was clearly opposed to the records in the upper part of the table where it was shown that oil extracts from pale fins had commonly given such reactions. If a pale fin yields an extract that will blanch a spot on a dark fish why will not a whole skin from a pale fish do the same? It occurred to me after I had made the standardization determinations that the probable answer to this question had to do with the concentration of the extracts. Possibly the oil extract from the skin was more dilute than that from the fins and hence the failure of the former extract to produce a pale spot. I therefore repeated this test and instead of extracting one pale dogfish skin with olive oil, as I had formerly done, I extracted three such with ether in a Soxhlet apparatus. These together yielded a residue of 0.8 g. of oily material. On mixing this residue with an equal volume of Ringer's solution and injecting 0.05 cc. of it into three dark pups pale patches appeared in every instance. I am therefore convinced that my first tests with skin extracts were made with too dilute a mixture and that when a strong skin extract is made it is as effective for blanching as the extracts from the fins. If the fin which shows a striking color change yields an effective extract, the skin of the flanks and dorsum which also changes color ought likewise to yield a similar product and apparently it does.

While these extractive operations were in progress other parts of the dogfish's body not previously tested were tried out. Soxhlet ether extracts of the brain and spinal cord were made and yielded relatively large amounts of residue which, however, when injected had no influence on the color of a dark fish. Dark fins were cut from fishes, dipped immediately in boiling water to kill the skin in the dark phase and prevent

gradual blanching, and then extracted. These yielded the usual amount of residue, but this residue even at full strength failed to elicit any color change in pale pups. Such results show conclusively that the blanching produced by the extract from pale fins cannot result from a material extracted from the cartilage, muscle, blood, etc., in the fin but must come from that part of the fin concerned with the actual color change, for that part is the only one in which the pale and the dark fins differ.

During the season in which these tests were made the fins of about 150 smooth dogfishes were dried and extracted and the residues studied. Through the kindness of Dr. E. L. Martin of the Harvard Chemical Laboratory much of this material was subjected to chemical fractioning with the view of ascertaining, if possible, something of the nature of the concentrating neurohumor. Dried fins were sent from Woods Hole to Cambridge and were then pulverized and extracted in a Soxhlet apparatus with anhydrous, pure ether for 36 hours. The yellow etherial extract thus obtained was put under reduced pressure for the evaporation of the ether and the resulting semi-solid, light-brown residue was sent to Woods Hole for testing. On injecting it into dark dogfishes it was found to excite the characteristic pale spots and it was thus shown to contain, as might have been expected, the concentrating neurohumor.

Further attempts were then made in Cambridge to ascertain something of the stability of the neurohumor concerned. Residues of the kind described were heated in a steam bath for ten minutes with four per cent sodium hydroxide. After extraction with ether and evaporation under a vacuum, the oily residue thus obtained was found to be fully effective in inducing pale spots in dark fishes. The alkaline fraction from this process was neutralized with hydrochloric acid, extracted with ether, washed with water, and dried. The slight residue thus obtained had no effect on the color of a dogfish into which it was injected.

A second extraction residue was washed three times with

two per cent sodium hydroxide then three times with two per cent hydrochloric acid and finally with water. On drying it with anhydrous sodium sulphate and extracting with ether a semi-solid material was obtained with a melting point between 80° and 100° C. When this material was injected under appropriate circumstances into a dark dogfish it was found to induce the formation of small, faint, pale spots. Purification by two additional ether extractions left the material still effective as a concentrating agent. The hydrochloric acid fraction from this test, after appropriate treatment and extraction with ether, yielded only an ineffective residue. In the course of these extractions a considerable amount of white flaky material was recovered which on purification showed the properties of cholesterol. When this substance was dissolved in olive oil and the mixture injected appropriately into dark dogfishes no pale spots appeared. Cholesterol apparently has no part in these reactions.

These tests, for which I am greatly indebted to Dr. Martin, together with information already accumulated permit a certain rough description of the concentrating neurohumor to be made. It is a substance soluble in olive oil and in ether, but not in water. It can resist heat to 110° C. It is not decomposed by weak alkali nor by weak acid. It must therefore be regarded as a relatively stable compound. To hazard a guess as to its relation to other organic compounds would perhaps be premature, but its properties point to the possibility of its being one of the sterols, a class of bodies the significance of which in animal and plant activities is rapidly coming to be recognized (Fieser, 1936).

9. Discussion

The three selachians upon which the present paper is based possess melanophore systems which are in a measure individual. From the standpoint of color responses *Squalus* is relatively inactive, *Mustelus* and *Raja* active. In all three the dark phase is due to a neurohumor from the intermediate lobe of the pituitary gland. In *Mustelus* and in

Raja this hormone fluctuates with the state of the environment, but in *Squalus* there must be a fairly persistent flow of it irrespective of the surroundings thus keeping this dogfish more or less continuously dark. The pale phase in these fishes is more diverse. In *Mustelus* it is due to the direct action of concentrating nerves on the melanophores and very probably to nothing else. In *Squalus* some individuals apparently never blanch at all; others blanch slightly as a result of direct nerve action. In *Raja* blanching is unassociated with nerves and with neurohumors. It appears to be due to the absence of the dispersing hormone and to no other condition. These summarizing statements indicate how diverse the melanophore systems of these three elasmobranchs are.

In the so-called active members of the group, *Mustelus* and *Raja*, the change from pale to dark and the reverse require hours or even days for full completion. Such changes cannot be regarded therefore as effective means of adapting these fishes to their surroundings. At best they fit these forms to the general tone of their environment without meeting the details of such a setting quickly and accurately as, for instance, the chromatophore systems of many flatfishes do. This sluggishness reflects the general character of a system built on the basis of water-soluble neurohumors, the hydrohumors, as contrasted with one which is more predominantly nervous and acts through immediately applicable lipohumors. These distinctions have already been indicated by Hogben (1936) in his brief allusions to the temporal phase of this subject.

In many respects, however, Hogben's view (1936) of the plan of action in melanophore systems is strangely at variance with much that has been recently discovered in this field. His statement that it is now firmly established that the coördination of chromatic response in reptiles is due to the direct innervation of their pigmentary effector organs ignores completely the important part played by the pituitary secretion in, for instance, *Hemidactylus* (Noble and Bradley,

1933) and *Anolis* (Kleinholz, 1935). And further his declaration that the color changes in elasmobranchs are under endocrine control and that peripheral innervation is intrinsically improbable in this group also ignores the nerve control that was shown some years ago to be present in *Mustelus*. It is unfortunate for Hogben's general statements that they should thus omit a consideration of contrary observations by reputable workers made in advance of his own publication.

His difficulties however are not only due to his ignoring of sound evidence; they result primarily from his insistence on a distinction in melanophore research that is rapidly disappearing. A decade ago it was usual to ascribe chromatophore control to either a nervous or a humoral agent. This attitude was in large part the outcome of Hogben's own work and was a very important step forward. But the investigations of the last few years have made it progressively clear that this distinction is no longer valid. The excitation of chromatophores by nerves is due to activating substances given out by the nerves themselves; the excitation by hormones is caused by materials from distant endocrine glands brought to the chromatophores by the blood. In fact in some forms as, for instance, in *Ameiurus* the animal responds because both these influences work together: the action of a dispersing neurohumor from the adjacent nerves and that of another dispersing neurohumor carried from the distant pituitary gland to the color cells. In a word there is no real distinction between these two methods of excitation. In both, neurohumors are the effective agents; the question involved is merely one of the nearness or remoteness of the source (Parker, 1932, 1936d). From this standpoint the distinction of a nervous and a humoral excitation really vanishes and in consequence the question discussed by Hogben as to which of these two is the more primitive loses much of its meaning.

When the vertebrate melanophore system or better the chromatophore system as a whole, is regarded in the way just outlined, a new light is thrown on its operations. The

numerous neurohumors involved in color responses may be active in different species in such a variety of ways, singly or in combination, that an understanding is at once accorded to such differences as have been described in, for instance, the three elasmobranchs discussed in the present paper. Differences of this kind are not only thus apprehensible but are to be expected in animals the color changes of which are being studied. Notwithstanding the diversity which a conception such as this involves, the view here presented rests upon a reasonably unified basis which in the end is the application of the neurohumoral hypothesis to chromatophoral relations.

10. Summary

1. *Squalus acanthias* is a dark dogfish that shows little or no evidence of a pale phase. As it blanches somewhat on loss of its pituitary gland its general darkness indicates a certain continuity of pituitary secretion independent of its environment.

2. *Mustelus canis* and *Raja erinacea* show well marked dark and pale phases in response to changes in their surroundings.

3. The dark phase in these three elasmobranchs is due to a hydrohumor from the intermediate lobe of the pituitary gland whence it is carried in the blood to the melanophores. This substance, contained in commercial pituitrin and in intermedin, is different from the oxytocic and the pressor principles from the pituitary gland.

4. The pale phase in these fishes is due to the absence from the blood of any dispersing factor (*Raja erinacea*), or to the action of nerves (*Mustelus canis* and *Squalus acanthias* in part). In these elasmobranchs there is no evidence of a concentrating neurohumor such as the W substance (Hogben) believed to occur in *Scyllium* and in some species of *Raja*.

5. Adrenalin blanches *Mustelus canis*, *Squalus acanthias*, and *Raja erinacea* but probably plays no part in the natural paling of these fishes.

6. The pinkness of pale elasmobranchs may be as much

due to the exposure of the dermal blood-vessel by pigment concentration as to the absence of a pressor factor.

7. The concentrating neurohumor in such elasmobranchs as *Mustelus* and *Squalus* is not carried by the blood; it is a lipohumor. It is soluble in olive oil, in ether, but not in water. It resists heat to 110° C., the action of sodium hydroxide and of hydrochloric acid. It is a relatively stable compound, possibly a sterol, but it is not cholesterol.

8. The color changes in elasmobranchs are slow in accomplishment involving hours and days, a condition associated with their usual means of excitation, chiefly hydrohumors.

9. In experimental operations on cold-blooded animals a mixture of broken ice and seawater or freshwater is a better means of stupefaction than drugs. Recovery from cold is more immediate and complete than recovery from drugs.

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FEEDING RATE OF CALANUS FINMARCHICUS IN RELATION TO ENVIRONMENTAL CONDITIONS[1]

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Objectives

The amount of food available to a plankton-feeding animal is determined by the concentration of suitable food material in the water, and by the rate of the animal's feeding activity. The calanoid copepods, like many other zoöplanktonts, are generally considered to feed by filtering out particles from a current of water generated by the animals (Cannon, 1928). By determining the number of food organisms removed by an animal from a suspension of known concentration, the volume of water which has been filtered clear of the organisms can be calculated and, if the chemical composition of the organisms be known, the amount of nutriment made available to the animal may be estimated. Preliminary measurements of the filtering rate of *Calanus finmarchicus* have been reported by Fuller and Clarke (1936). Further investigation of changes in the feeding rate induced by varying environmental factors of ecological importance was expected to yield information useful in the quantitative study of aquatic food cycles. Diatom concentration, light and temperature were expected to be variable factors in the sea and were chosen for study.

Methods

In the experiments here reported the rate of feeding of the copepod *Calanus finmarchicus*, collected in Vineyard Sound near the whistle buoy, was measured in a suspension of the diatom *Nitzschia closterium* (Plymouth strain). It seems probable that *Nitzschia* is a suitable food for *Calanus*, as Crawshay (1913–15) kept individual copepods alive for as long as 80 days in persistent cultures of this diatom. Allen and Nelson (1910, p. 470) reared *Calanus* from eggs to copepodid stages in a mixed culture in which *Nitzschia* was predominant.

Three stage V *Calanus* were placed in 15 cc. of sea water containing a known concentration of diatoms. Changes in concentration were followed for two to four days, counts being made in a hemacytometer.

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A series of counts on successive samples showed fair agreement with the theoretical Poisson distribution. The small excess variation found is attributed to the difficulty of shaking the diatoms to obtain even distribution without injuring the copepods. Enough diatoms were counted for each sample to give a result statistically valid to between 5 and 10 per cent. Under the experimental conditions this is the maximum precision obtainable. In these experiments a counting error of 10 per cent causes a discrepancy of about 30 per cent in the estimation of the filtering rate. Obviously only large variations can be satisfactorily studied.

TABLE I

Feeding rate at different diatom concentrations

Expt. No.	Date begun	Cells per cc.		Duration	W_{24}	ΔN_{24}
		C_1	C_2			
				hours	*cc.*	
47	Aug. 18	1,875	1,140	42	1.32	2,100
48	Aug. 18	1,875	1,155	42	1.28	2,060
63	Aug. 23	19,000	15,400	38	.66	11,400
64	Aug. 23	19,000	13,100	38	1.17	16,100
14	July 9	64,700	27,000	81	1.30	55,000
15	July 9	64,700	27,700	81	1.25	55,000
71	Aug. 26	190,000	147,000	38	.81	136,000
72	Aug. 26	200,000	133,000	38	1.29	212,000
11	July 3	335,000	86,000	84	1.61	356,000
10	July 3	375,000	220,000	84	.43	221,000
8	June 29	390,000	130,000	84	1.32	371,000
7	June 29	410,000	230,000	84	.60	256,000
				Average	1.09	

Calculation of the amount of water, W_x, swept free of diatoms by each copepod in x hours was made by means of an equation derived as follows:

$$dN = -dWC \tag{1}$$

$$dC = dN/V \tag{2}$$

$$dW = VdC/C \tag{3}$$

$$W_x = V \ln C_1/C_2. \tag{4}$$

N represents the number of diatoms per copepod; V the volume of water per copepod; C_1 and C_2 respectively the concentrations of diatoms at the beginning and end of the period of x hours.

The number of diatoms eaten in x hours per copepod, ΔN_x, is given

by the equation:

$$\Delta N_x = V(C_1 - C_2). \tag{5}$$

Parallel control suspensions were always counted to determine whether the diatom numbers were varying independently. If a control changed greatly during the experimental period, the results of the corresponding experimental series were discarded. If the change was small, the final concentration of diatoms in the control was substituted for C_1 in equations (4) and (5). This substitution assumes that the diatoms in the experimental containers increased or decreased independently exactly as those in the control. This is, of course, only an approximation.

Observations were also made on the production of fecal pellets. Since these pellets vary greatly in size no quantitative relationship could be obtained between the number of diatoms ingested and the number of pellets ejected. However, the formation of these excreta was a useful check on the reduction of diatom numbers observed directly.

Effect of Changing Diatom Concentration

Table I gives the results of experiments with different concentrations of diatoms. In the lowest concentration the diatoms were concentrated by the Nielsen-von Brand (1934) method before counting. These experiments were carried out at 13° C., and the animals were shielded from direct sunlight. The values for W_{24} and N_{24} in the table represent means over a period of several days. Diatom concentration often remains stationary for a day or more, thus indicating that feeding is not a continuous process. The maximum rate of filtration is higher than these values. The highest rate observed was in Experiment 11 where over a period of 14 hours W equalled 2.87 cc. which would give a W_{24} value of 4.9 cc. There appears to be no correlation between the concentration of food and the filtering rate. A comparison of the filtering rates of animals collected at different times during the summer yields no greater differences than a comparison of animals collected at the same time and used in parallel experiments (e.g. Nos. 10 and 11). The indication is that *Calanus*, though it sometimes does not feed actively, under otherwise constant conditions filters a definite volume of water per day, and obtains nutriment in direct proportion to the concentration of food particles.

Effect of Light on Feeding Rate

In certain experiments there appeared to be a diurnal feeding rhythm, removal of diatoms taking place most rapidly at night. This

is in accord with the observation of Marshall (1924), who notes that *Calanus* captured by tow-net hauls in the early morning had full guts, while those caught later in the day often had no food in their alimentary tracts. Figure 1 represents the course of two experiments (8 and 11) which show this rhythm. It is not, however, an invariable

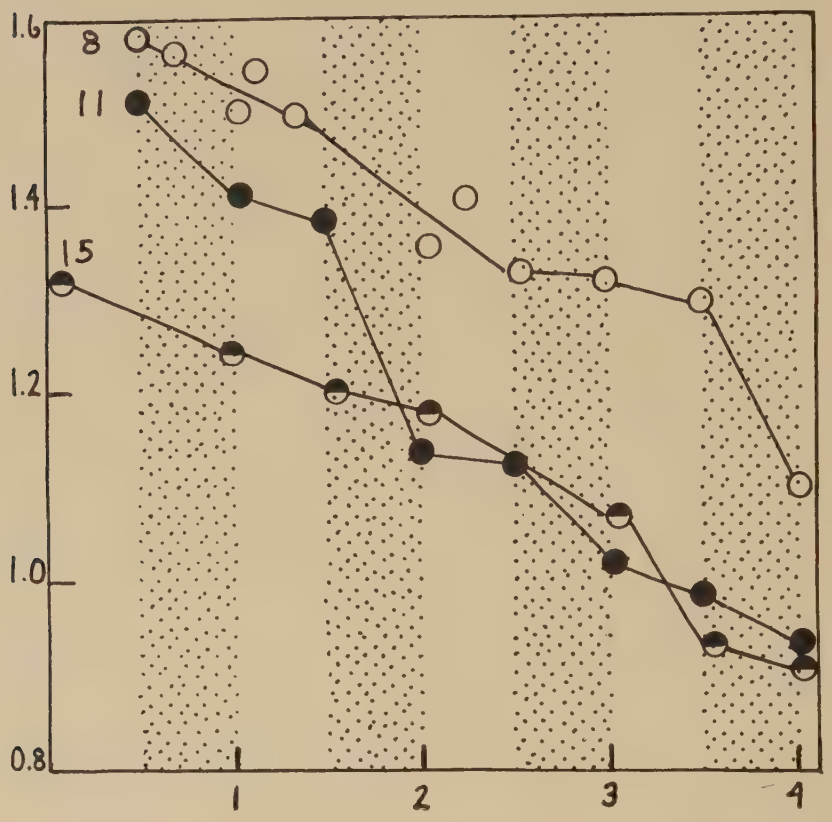

FIG. 1. Diurnal feeding rhythm of *Calanus*. Stippled areas represent hours between 8 P.M. and 8 A.M. The scale of Experiment 15 is adjusted by adding 0.5 to logarithms of cell numbers. Ordinates: *Logarithm-cells per 0.1 cu. mm.* Abcissæ: *Time in days.*

effect, as is shown by the course of Experiment 15, also shown in Fig. 1. Marshall likewise found that during the summer feeding occurred during the day as well as at night.

Experiments 26 and 32 differed from those reported above in being kept in darkness. Table II summarizes the results of these two experiments.

TABLE II

Feeding rate in dark

Expt. No.	Date begun	Cells per cc.		Duration	W_{24}	N_{24}
		C_1	C_2			
				hours	*cc.*	
26	July 16	54,000	32,000	90	.27	45,000
				48*	.76*	
32	July 30	61,000	20,000	65	1.8	76,000

* Animals actually fed only during last 48 hours of experiment. W_{24} value calculated for this period.

The results do not differ significantly from the average given in Table I, although there are admittedly too few cases to permit a definite answer. An attempt was made to study the effect of continuous light. The animals did not feed during the two days they were observed, but they were old stock in poor condition, and no reliance should be placed on this observation. Unfortunately it was impossible to collect more *Calanus* to make satisfactory experiments.

Effect of Temperature on Feeding Rate

Experiments were carried out at 8° C. and at approximately 3° C. The latter temperature was not precisely controlled as the containers were placed in a refrigerator in general laboratory use. Both series were kept in the dark.

Feeding is much slower at 3° but still goes on with the formation of small compact fecal pellets. The very low filtering rates observed in Experiments 75 to 79 may be explained by the fact that the animals used were collected late in the season when the *Calanus* population was receding rapidly, and had perhaps stopped eating. The filtering rate in Experiment 80, in which the same stock was used, is seen to be much slower than that in Experiments 55 and 56. The high value for W_{24} in the latter experiments seems to indicate that 8° C. is somewhat more favorable for feeding than 13°. Excluding Experiments 75 to 80, the average values of W_{24} at 3°, 8° and 13° are respectively, 0.35, 2.83 and 1.09 cc.

Organic Nitrogen Content of Nitzschia and of Plankton

Through the kindness of Dr. Theodor von Brand, an analysis of the organic nitrogen content of *Nitzschia* was made by the method he has developed for small amounts of plankton (von Brand, 1935). *Nitzschia* contains 0.9 microgram of nitrogen per million cells. Assuming the carbon-nitrogen ratio in this diatom to be equal to that

generally found in marine phytoplankton, approximately 8 : 1, we have 7.2 micrograms of carbon per million cells. Analysis of the fecal pellets of *Calanus* fed on *Nitzschia* showed that 0.55 microgram of nitrogen appeared in the feces for each million cells ingested. Roughly, about half the organic nitrogen was retained by the copepods.

Marshall, Nicholls and Orr (1935) have calculated from measurements of oxygen consumption the daily nutritive requirement of a stage V *Calanus* in summer as equal to 13 micrograms of carbohydrate. Assuming all the nitrogen of *Nitzschia* to be in protein, and the excess carbon to be in fat, one may calculate the number of cells which would supply an equal amount of energy. If the protein is assumed to contain 16 per cent nitrogen and 50 per cent carbon; the fat to contain 75 per cent carbon, we have:

TABLE III

Effect of temperature on feeding rate

Expt. No.	Temp.	Date begun	Cells per cc.		Duration	W_{24}	N_{24}
			C_1	C_2			
	°C.				*hours*	*cc.*	
42	3°	Aug. 18	263,000	215,000	90	.38	64,000
43	3°	Aug. 18	263,000	223,000	90	.32	53,000
55	8°	Aug. 22	85,500	30,000	42	2.88	159,000
56	8°	Aug. 22	85,500	31,000	42	2.78	156,000
80	8°	Aug. 31	24,000	14,000	65	.98	18,500
(75, 76) (79)	8°	Aug. 31			85	.00	0

$0.9 \times 0.16 = 5.62\ \gamma$ protein containing $2.8\ \gamma\ C$.
$7.2 - 2.8 = 4.4\ \gamma\ C$ in fat
$4.4 \times 0.75 = 5.87\ \gamma$ fat.

Proteins and carbohydrates have equal energy values per unit of weight. Fat has 2.25 as great an energy content as carbohydrate. Calculating fat and protein in terms of carbohydrate, we obtain:

$$5.87 \times 2.25 = 13.2$$
$$\underline{5.6}$$
$$18.8\ \gamma$$ weight of carbohydrate equivalent in energy content to a million *Nitzschia* cells.

$$\frac{13}{18.8} \times 1{,}000{,}000 = 690{,}000$$ number of *Nitzschia* cells which would contain theoretical food requirement.

The maximum amount of water filtered per day (W_{24}) in any experiment was 2.88 cc. A concentration of 240,000 cells per cc. would be required if *Calanus* is to obtain its theoretical food requirement from this volume of water, even if all the organic matter is utilized. Probably this value should be doubled since only half the nitrogenous organic matter appears to be assimilated. In any case this is a much higher concentration of phytoplankton than ever occurs in nature, but since the size of phytoplankton cells varies so greatly, comparisons based on cell numbers are worthless. It is, however, possible to determine the organic nitrogen content of the particulate matter in sea water, and to compare this with the food requirements of *Calanus*. Table IV summarizes the results of two sets of analyses by Dr. von Brand of the particulate matter suspended in Vineyard Sound water. All macroscopically visible organisms were removed

TABLE IV

Organic N in particulate matter in Vineyard Sound water

Date	Depth	Temperature	N
	meters	*° C.*	*per liter micrograms*
July 2	0	17.8	15
	15	13.5	27
	30	9.1	13
August 14	0	20.0	38
	15	18.0	42
	30	12.0	19

from the August 14 samples before analysis. This was not done for the July 2 samples.

The maximum value found was 42γN per liter, a nitrogen concentration equal to that of a *Nitzschia* culture containing 46,700 cells per cc. This is so far above the average number of diatoms per cc. in Vineyard Sound—the figure is probably close to 100—that, even allowing for the fact that one large cell is the equivalent of many *Nitzschia*, it appears probable that the major portion of the particulate matter at this station was not in the form of diatoms. The remainder, detritus or other organisms, is presumably of great significance as a source of food.

Even in this region of high nitrogen content 2.88 cc. of Vineyard Sound water contained less than one-fifth the theoretical food requirement, and in all probability not over one-tenth this amount since half the nitrogenous matter is believed inassimilable, and some of the particles were probably too large or too small to be captured. Yet *Calanus* survives and grows in this region. Two explanations are

possible: (1) *Calanus* in nature requires less food than that calculated from laboratory experiments on oxygen consumption, or (2), *Calanus* in nature filters a greater volume of water and thus obtains more than the estimated amount of food.

Nutritive Requirements of Calanus

Knowing the rate at which *Calanus* feeds on *Nitzschia*, it should be possible to supply the animals with known concentrations of

Table V

Survival and moults of Calanus fed on Nitzschia

Expt. No.	Nitzschia cells/cc.	Initial population		Successful moults	Deaths in moult	Deaths not in moult	Percentage reaching moult	Average survival
		No.	Stage					
								days
B1	300,000	2	III	0	2	0	63.2	8.9
		12	IV	1	8	3		
		5	V	0	1	5		
B2	150,000	11	IV	1	3	7	33.3	9.7*
		4	V	0	1	3		
B3	30,000	14	IV	0	5	9	38.9	9.5
		4	V	0	2	2		
B4	15,000	8	IV	0	3	5	41.1	10.4*
		11	V	0	5	5		
B5	0†	10	IV	0	1	9	18.7	11.0*
		6	V	0	2	3		
B6	Harbor water	4	IV	0	3	1	60.0	7.2
		16	V	0	9	7		

* In each of these experiments one stage V still living after 19 days.

† All attempts to moult near end of experiment. Examination showed minute protozoa present. None in Experiments B1–B4.

diatoms, observe the minimum concentration at which growth takes place, and calculate the food requirement in terms of planktonic organic nitrogen. Experiments were set up in which 15 to 20 *Calanus* were placed in 250 cc. of Berkefeld filtered sea water containing definite concentrations of *Nitzschia*. The concentrations chosen together with the amount of nitrogen per cc. in each case were:

(B1) 300,000 cells and 0.27γN per cc. representing a concentrated food supply with the theoretical amount of nutriment contained in 2.5 cc.

(B2) 150,000 cells and 0.135γN per cc., half the above.
(B3) 30,000 cells and 0.027γN per cc. representing an approximation to the concentration of organic nitrogen found in Vineyard Sound.
(B4) 15,000 cells and 0.014γN per cc., half the above.
(B5) Berkefeld filtered water—no diatoms.
(B6) Water collected from Woods Hole Harbor.

The medium was changed daily except Sunday, and dead animals were removed at each observation period. Animals were transferred

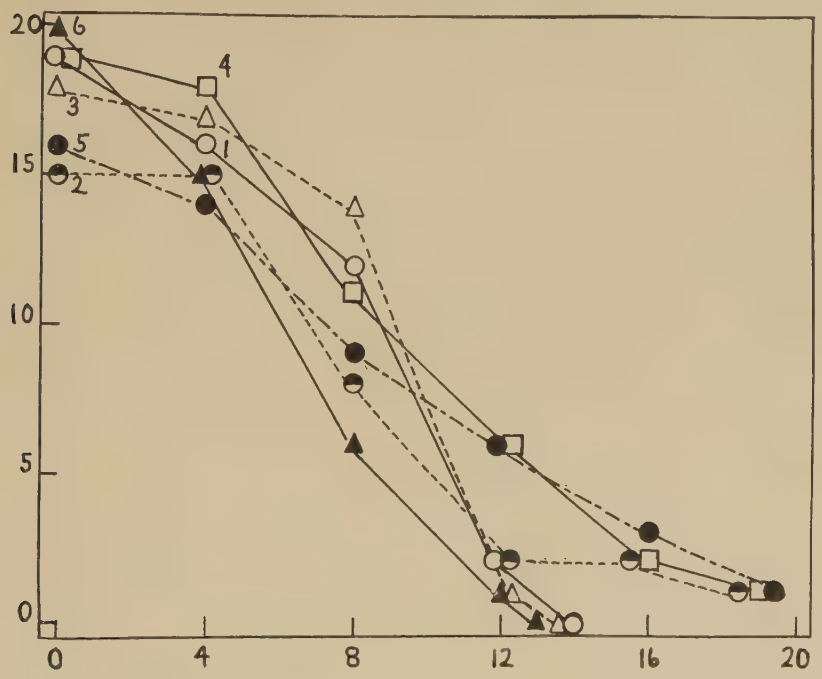

FIG. 2. Series B. Survival of *Calanus* fed on different concentrations of *Nitzschia*. B1—300,000 cells/cc.; B2—150,000 cells/cc.; B3—30,000 cells/cc.; B4—15,000 cells/cc.; B5—Berkefeld filtered water; B6—water from Woods Hole Harbor. Ordinates: *Number of survivors*. Abcissæ: *Time in days*.

by means of a lifter of bolting cloth or in a wide-mouthed pipette. In order to study growth, stage IV *Calanus* were used insofar as they were available. Survival was uniformly poor compared with experiments which were reported previously by Fuller and Clarke.[2]

These experiments are summarized in Table V and Figs. 2 and 3.

[2] Clarke and Zinn found that in both 1935 and 1936 there was a sharp reduction in the *Calanus* population in Vineyard Sound during the latter part of August. The animals were either being carried away, or were dying off. This may explain the high mortality in these experiments.

The previous observation that ecdysis is a critical period for *Calanus* is again brought out by the data for "deaths in moult." It is believed, however, that the attainment of the moulting stage represents true growth, and indicates that the animals are feeding, since ecdysis does not occur in starved animals (Fuller and Clarke, p. 312). If the attainment of the moulting stage—whether successful or not—be taken as the criterion, growth is most rapid in the most concentrated diatom suspension and in harbor water in which media 63.2 and 60 per cent, respectively, of the original population reached the moulting stage. Growth rates in the other diatom suspensions are essentially equal

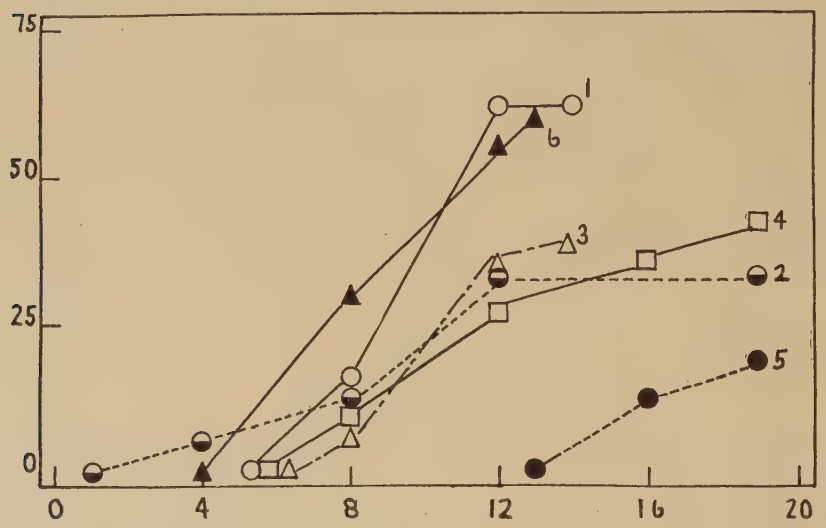

FIG. 3. Series B. Percentage of original population of *Calanus* attaining moulting stage when fed different concentrations of *Nitzschia*. Symbols as in Fig. 2. Ordinates: *Percentage of moults*. Abscissæ: *Time in days*.

(33–41 per cent), while the few moults which occurred in Berkefeld filtered water (19 per cent) are probably due to a protozoan infection of the culture which developed during the last few days of the experimental period and furnished a food supply for the copepods. There is a definite negative correlation between the average survival period in each experiment and the percentage of animals attaining the moulting stage. This is attributed to the fact that when growth is slower, the critical period of moulting is reached later and average survival increases.

If each *Calanus* captured daily the diatoms from 2.5 cc. of water, then in Experiment B4 in which some growth obviously took place, each individual obtained per day only 37,500 cells, 0.034γN, and

between 8 and 16 per cent of the food requirement calculated from oxygen consumption. The higher value assumes all the nitrogenous matter to be utilized; the lower value is based on the assumption that one-half is utilized.

Discussion

The filtering rate of *Calanus* in these experiments was less than that found by Fuller and Clarke using carmine particles, the previous value at 13° C. being 5.61 cc. per day against 1.09 cc. reported above. As the carmine particles tended to settle and were more difficult to count, the present values are the more reliable. Harvey (private communication) has found filtering rates of from 50 to 100 cc. per day using the larger diatoms *Lauderia* and *Ditylium*, though his values are based on only a few experiments. It seems probable that large particles are captured more readily, though the carmine particles mentioned above were somewhat smaller than *Nitzschia*.

Whether these varying results represent actual differences in the rate of filtering is a moot point. Possibly the variance depends upon the efficiency with which the maxillary bristles strain out particles of different sizes and shapes. It may be that small cells, such as *Nitzschia*, pass between the bristles so that a copepod retains only a small percentage of the *Nitzschia* in the water current which it generates. This is the author's view. On the other hand some investigators believe that copepods possess other food-capturing mechanisms besides filtration.

Lowndes (1935), basing his opinion on anatomical grounds, and on observation of living unrestrained animals, states that feeding of the calanoid copepods cannot be merely automatic, non-selective filtering, but involves the finding and grasping of food particles. *Calanus* has two distinct types of movement: (1) saltation in which propulsion is furnished by the antennules and swimming feet, and (2) a slow glide in which the motive force comes from the vibration of the mouth parts. It is the latter which furnishes the feeding current. Often this species remains suspended quietly in the water for several minutes. Since the eye of copepods is not capable of forming images, recognizance of food material would have to be chemical or tactile in nature. In a turbulent fluid medium, only tactile stimuli would be serviceable in precisely locating food. Saltations might enable a copepod to try out different regions for food, the filtering mechanism being called into play only when food was encountered. One would thus expect more filtering where food was abundant since more particles would be encountered. On the other hand, the rate of feeding might be controlled by the amount of food ingested, so that filtering would slow

down when food was abundant and speed up when food was scarce. No tendency towards a change in the filtering rate was shown. Harvey's results agree in this respect. Two conclusions are possible: (1) the rate of filtering is independent of the amount of food ingested or encountered; (2) even in the highest diatom concentrations used in these experiments there was insufficient food so that filtration was maintained at a maximal rate. Since in many experiments (e.g. 7 and 8) diatoms were present in concentrations much higher than are ever found in nature, alternative (2) is ruled out. The evidence definitely favors the theory that filtration is an automatic process independent of the concentration of food, though its rate is modified by physical factors in the environment.

These factors insofar as they have been studied may be considered in relation to the ecology of the species. The suggestion of a diurnal feeding rhythm is nicely correlated with the habit of vertical migration in this species which rises to the surface at night, and sinks below this rich food zone during the day. Neither phenomenon is absolutely regular. Probably both are dependent upon the physiological state of the animal which conditions its response to light (see Clarke, 1934). The ability of *Calanus* to feed at temperatures as low as 3° C. and its high rate of filtering at 8° indicate a physiological adaptation to life in the colder parts of the ocean.

The question of the food requirement of *Calanus* is perhaps of greatest fundamental importance, since the rôle of the food supply in the regulation of the *Calanus* population can only be determined when the minimum requirements for metabolism and growth are known. The discrepancy between the requirement calculated from oxygen consumption measurements and that estimated from measurements of the filtering rate and the concentration of particulate matter in the sea has been mentioned above.

It was hoped that the experiments of Series B reported herein would resolve this difficulty, but the heavy mortality occurring in them makes definite conclusions unsafe. However, a higher percentage of copepods attained the moulting stage in Experiment B4 with a minimum concentration of diatoms, than in Experiment B2 with ten times as many, although there was one successful moult in the latter experiment against none in the former. Presumably each copepod in Experiment B4 received not over one-sixteenth of the food requirement calculated from oxygen consumption. It is unlikely that the filtering rate in B4 was sixteen times greater than in any of the experiments in which the rate was measured. Thus it is probable that the minimum nutritive requirement for growth is less than previously believed,

though it is as yet impossible to set a definite figure. Why higher concentrations of food have so little effect on the rate of growth is problematical unless the concentration in B4 itself is well over the required minimum. Another problem is the reason for the rapid growth of *Calanus* in harbor water. Possibly qualitative as well as quantitative differences in the food supply are involved in this case.

When larger particles serve as food the effective filtering rate is probably higher. If so, the concept of the feeding rate taken at the beginning of this work—namely the volume of water filtered per unit of time—must be modified. Instead the feeding rate must be considered as the number of particles of a given type captured per unit of time when present in a given concentration.

It follows that the investigation of the minimum concentration of food which will support life and growth in *Calanus* and in other species must employ several types of food organisms. The problem is a complex one, for it is possible that the metabolic rate of *Calanus* varies with the amount of food taken in as well as with other environmental factors.

Summary

(1) The filtering rate of *Calanus finmarchicus* on the diatom, *Nitzschia closterium*, was measured under different conditions of diatom concentration, light and temperature, by observing the reduction in concentration of the diatoms. Change in diatom concentration had no effect on the rate of filtration. There was some evidence of a diurnal feeding rhythm with greater activity at night. Feeding was most rapid at 8° C., slower at 13° and 3°.

(2) Studies on the growth of *Calanus* supplied with different concentrations of diatoms indicated that the food requirement is less than has been calculated from oxygen consumption measurements. This is also borne out by comparing the amount of particulate organic matter in the sea with the rate of feeding measured in the laboratory.

(3) The view that the feeding activity of *Calanus* is automatic filtering is favored by these experiments.

(4) Approximately one-half the organic nitrogen content of *Nitzschia* is in a form available to *Calanus*.

(5) These results are correlated with the ecology of *Calanus* as studied in the field.

The author is indebted to Dr. George L. Clarke for many helpful suggestions, and to Miss Margaret Frothingham for technical assistance.

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BACTERIA AND THE PHOSPHORUS CYCLE IN THE SEA[1]

CHARLES E. RENN

(From the Woods Hole Oceanographic Institution, Woods Hole, and the Biological Laboratories, Harvard University)

Marine bacteria, growing and multiplying rapidly under favorable conditions, are potential accumulators of the sea's labile organic matter. Lohmann (1911) has estimated that they may bind as cell substance each year from six to three hundred times the annual production of slower growing nannoplankton feeding upon them.

It is surprising, then, to discover, as Fischer (1894) and many others since have pointed out, that the bacterial population of the sea and large fresh-water lakes is very low—rarely exceeding a viable count of a hundred at the surface and extending through a lesser range in the depths (Birge and Juday, 1922; Reuszer, 1933). Lohmann found the mass of bacterial cells in sea water to represent an insignificant fraction of the nannoplankton; and it may be calculated, making generous allowance for non-viable cells, that the amount of phosphate, nitrate, or other nutrient substance bound by bacteria is immeasurably small. Thus, a million cells per cubic centimeter, at least a thousand times the likely bacterial population, would be equivalent to less than 3 mgm. PO_4 per cubic meter (Buchanan and Fulmer, 1933, pp. 69–71). Bacterial cell substance is notoriously rich in phosphorus, but it is apparent from their small numbers, that bacteria do not compete effectively for the sea's limited store of this element. Do these small numbers also indicate a low limit to their activity in the breakdown of debris and the regeneration of inorganic nutrients?

If Fischer's observations regarding the short life of marine bacteria are valid (he estimated their average viable span to be in the order of a half hour), then Lohmann's emphasis on their rôle as converters of organized material rather than accumulators gives a sound picture of their relations in marine economy. Rate of growth, length of the viable period, and rapidity of autolysis after death become critical factors in determining their value as regenerating agents.

Several experiments make it seem plausible that short-lived bacteria are active in phosphate regeneration, and offer confirmation for the smaller, inter-seasonal phosphorus cycles indicated in the investigations

[1] Contribution No. 133 from the Woods Hole Oceanographic Institution. Contribution from the Bermuda Biological Station for Research, Inc.

of Harvey and co-workers (1935) on plankton production, and remarked by Seiwell (1935). When specimens of sea water are stored in bottles at room temperature the bacterial population therein rises in two or three days to a level much higher, from a thousand to a hundred thousand times, than that of natural waters. This sudden increase is followed by a precipitous drop in viable numbers to a persistent low count (Waksman and Renn, 1936). That such unrestricted development of bacteria may withdraw appreciable quantities of phosphate from

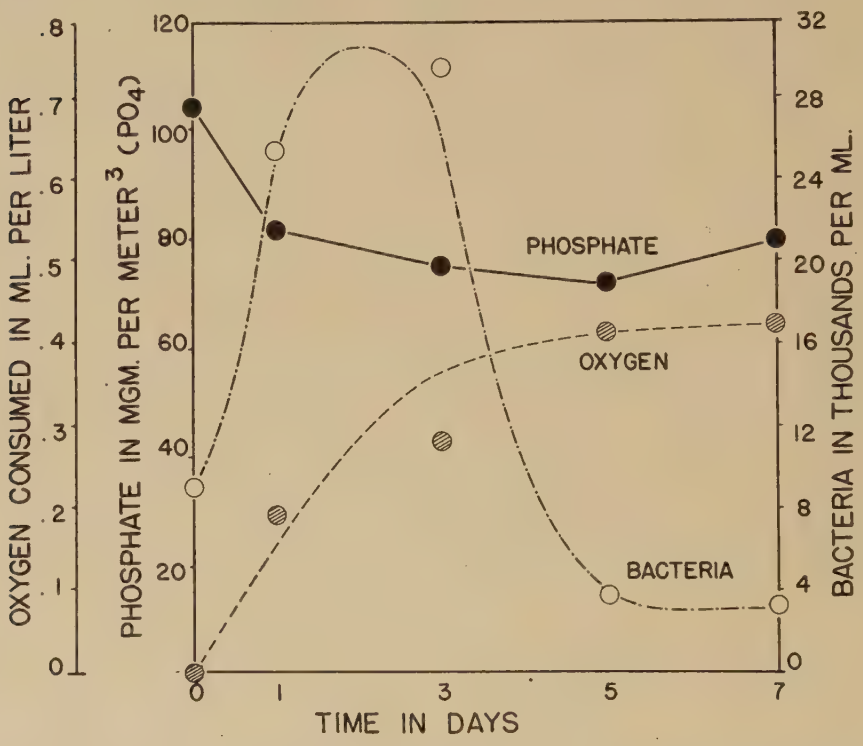

FIG. 1. Showing assimilation and regeneration of phosphate by bacteria in stored samples of sea water from Woods Hole Harbor—July 10, 1935. Phosphates in triplicate, other determinations in duplicate.

sea water is shown by the decreasing concentrations in unpreserved specimens taken for analysis during the first two or three days of storage.

The first experiment was designed to relate these two behaviors—increase in bacterial numbers and assimilation of phosphate. Water from the mouth of Woods Hole Harbor was enriched with K_2HPO_4 to bring the phosphate content to about 100 mgm. per cubic meter, filtered

through quartz sand, and dispensed into sterile, standard, oxygen demand bottles. These were stored in the dark at room temperature for varying lengths of time after which phosphate, bacterial number, and dissolved oxygen determinations were made. Figure 1, incorporating the results, clearly shows the rapid decrease in phosphate during the first three days of storage as noted before. Simultaneously the bacterial numbers and oxygen consumption reach their maximum. After three days the viable bacteria fall to a low level, and the oxygen uptake

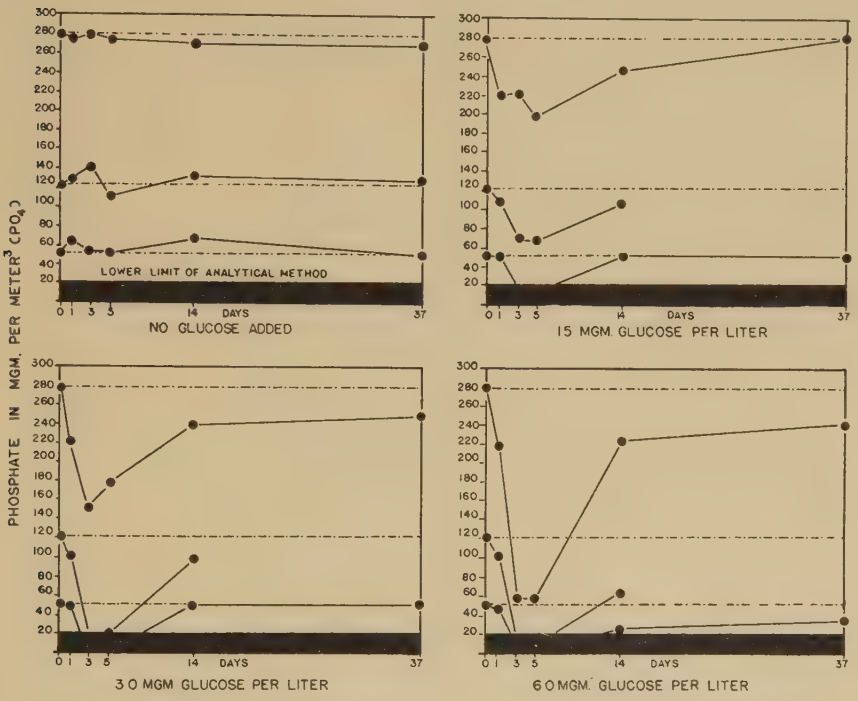

FIG. 2. Showing assimilation and regeneration of phosphate in stored sea water from off Bermuda, January, 1936. All determinations in triplicate.

slackens off. On the seventh day there are signs of phosphate regeneration.

There is, then, an interval of two or three days in which 20–25 mgm. of phosphate per cubic meter is bound as non-viable bacterial cells. (The count of viable cells has qualitative value only, indicating the phase of growth rather than actual numbers. Assimilated phosphate is held by a quantity of bacterial cells that is roughly proportional to the organic carbon oxidized during rapid growth—in this case an equivalent of 0.75 mgm. glucose per liter.) It has been pointed out that the length

of time that phosphorus may be held by bacterial cells synthesized during decomposition of organic phosphorus compounds is significant in estimating their activity in phosphate regeneration. If this is long, then the process is retarded, but if, as this preliminary experiment suggests, the cells lyse within a short time, the turnover through their agency may be rapid.

In January, 1936, there was an opportunity to study the complete cycle of bacterial assimilation and regeneration under particularly favorable conditions, using the waters about Bermuda and the facilities at the Bermuda Station for Biological Research. The waters in this region are characteristically poor in phosphate, organic phosphorus, and available carbon—components that had proven troublesome in attempts to extend the experiments in Woods Hole. (A number of determinations showed the total phosphorus in shallow bays between St. Georges and Shore Hills to be less than 40 mgm. PO_4 per cubic meter.)

Sea water, taken from the surface about three miles southeast of Castle Roads, was filtered through quartz sand (imported), and enriched with varying amounts of phosphate and glucose, and a uniform excess of nitrate and iron. This was dispensed into a series of three-liter bottles and stored in the dark at room temperatures of 19° to 21° C. At intervals specimens were taken for phosphate analyses.

Results of the periodic inorganic phosphate analyses on the prepared, stored water are given in Fig. 2. Phosphate assimilation is complete in about five days, by which time it may be assumed bacterial growth has passed its maximum. Regeneration follows almost at once —rapid at first, and then leveling at fourteen days toward completion. Most of the phosphate is regenerated within this time, but a fraction, ranging from an eighth to a third, and greatest where relatively large quantities of glucose have been added, is still bound at the end of thirty-seven days when the experiment was terminated. It seems clear that bacterial cells do not bind phosphorus for more than a few days under storage conditions.

If autolyzing bacterial cells liberate phosphorus as phosphate there always exists the possibility that diatoms and other phytoplankton may similarly bring about direct regeneration. Two attempts to demonstrate direct regeneration gave negative results, but it will be recognized from the methods followed that the mechanism is by no means disproved. Ten-day cultures of *Nitzchia* grown in synthetic media were filtered and washed free of inorganic phosphate on a Seitz filter. The cells were suspended in 200 ml. of distilled water and washed on a second filter with 800 ml. of sea water, the lysate passing into a sterile aspirator

bottle fitted with tubes for periodic sampling. Phosphate analyses at intervals of 14, 20, and 48 hours indicated no increase whatever in inorganic phosphate content.

A modification was arranged in which cultures of *Nitzchia* were washed on the Seitz filter, removed with a thin layer of the filter pad, lysed in distilled water for two hours, suspended in ten volumes of sea water, and allowed to stand. After three and eight hours, respectively, specimens were centrifuged and analyses made. These yielded no measurable amounts of phosphate.

Discussion and Summary

Bacteria, despite their potentialities as rapidly multiplying organisms, do not compete with higher phytoplankton for phosphate. Many factors may be suggested to account for their low numbers, but short life and brief viability period undoubtedly play a part. Under storage conditions where their rapid growth is favored they assimilate significant quantities of phosphorus, but this is quickly regenerated following their death. This suggests that the numbers of viable cells in natural water is not a complete index of bacterial activity, and that the efficiency of the organisms as agents of regeneration is inversely proportional to their life span.

The relations of the rapid growth phase, short period of maximum viable population, and the declining phase are not unique in marine bacterial cultures but are characteristic of bacterial populations in general (Buchanan and Fulmer, 1933, pp. 69–71). The curve representing them is the resultant of many growth and death curves over much shorter intervals, so that the number of cells actually produced during three, five, seven or fourteen days is indeterminately greater than the population at any one time.

Many other mechanisms for phosphate regeneration may be active in the sea. These experiments demonstrate one possible system, involving the agency of bacteria. They also offer an explanation for the insignificant amounts of bacterial cell substance in the nannoplankton.

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CHANGES IN THE INVERTEBRATE COMMUNITY OF A LAGOON AFTER DISAPPEARANCE OF THE EEL GRASS

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Introduction and Description of Area

In 1923 while the eel grass, *Zostera marina,* was flourishing in suitable areas around Woods Hole, W. C. Allee completed a study of the animal communities of the region, and described in some detail the one characteristic of the eel grass areas. In 1931 practically all the Woods Hole eel grass was killed by a mycetozoan parasite, and today it is still very scarce. Interest in the possible changes in the animal community led to a new survey made in early September, 1936.

The area which Allee found to show the eel grass community best is a shallow lagoon in the Northwest Gutter, a channel running between Naushon and Uncatena Islands. In 1923 the portion of this lagoon which was always covered by at least 30 centimeters of water was filled with a dense matting of eel grass. In the summer of 1936 the lagoon floor was a vast extent of muck without any plant covering. The eel grass was gone except for one or more small patches about one square meter in area, and the many dead rhizomes still in the mud were the only evidence of its former abundance.

The Invertebrate Community Before and After

In his most detailed analysis Allee subdivides the area into two communities, but in his general quantitative faunal list he treats it as a single unit, and for this general comparison I shall do the same. Formerly, the animals of the area were of four types: those living upon the plants, those living among them, those upon the surface of the mud, and those burrowing among the roots in the mud. Characteristic forms of the first type were the anthozoan, *Sagartia luciae,* the bryozoan, *Bugula turrita,* and the gastropods, *Bittium alternatum* and *Littorina litorea.* Swimming forms belonged to the second type; the annelid, *Podarke obscura,* was frequently abundant, and the small shrimp, *Virbius zostericola,* and the scallop, *Pecten irradians,* were numerous. The third group, those living just on the surface of the mud, was composed of crustacea and molluscs. The annelid, *Scoloplos fragilis,*[2] was the most abun-

[1] Contribution No. 134 of the Woods Hole Oceanographic Institution.

[2] This form was first identified in part as *Scoloplos acutus:* see Allee, '34, and Dawson, '31, for discussion of this point.

dant and characteristic of the group burrowing in the mud. Now, only the last two of these major types are to be found. My observations and collections, summarized in the second column of table I, indicate that, of the characteristic animals of the first two types, *Littorina litorea* and certain crustacea moved to the surface of the mud when the eel grass went out, and the others disappeared completely. No such significant change occurred in the bottom forms. Table I allows a comparison of the occurrence of the important members of the population before and after the disappearance of the *Zostera.* A decline of about one-third of the number of species after the extermination of the grass is evident; the total decreased from 55 to 36 and no species new to the area since 1923 were noted. The short period of collecting for the 1936 study does not seem an important factor in this.

Allee's faunal list was compiled from the collecting reports of over 50 crews of students in the course in Invertebrate Zoology at the Marine Biological Laboratory. Each crew reported a species as either present or absent in their collections, and it is reasonable to assume that the number of crews reporting a species was roughly proportional to the abundance of the species, although also in part proportional to its conspicuousness.

A comparison of the total population of the area before and after the epidemic would be of interest in regard to possible changes in the total number of individuals and in their total mass, but the 1923 data are not suitable for this.

Comparison with Conditions on the English Channel

The results of this study on the Massachusetts coast should be compared with the observations of Marcel Prenant regarding the effects of the disappearance of *Zostera marina* in the Morbihan, a bay on the southern coast of Brittany. The epidemic left only a few scattered plants of *Z. marina* there, and *Z. nana* and *Chorda filum* have only partially replaced it. There the effects of the loss have been greater than those near Woods Hole. The disappearance of the mat of vegetation permitted increased current scouring and hence changes in the composition of the sediments. Epiphytic forms diminished in number for lack of support, but they are present still where *Z. marina* is now found. Decrease in the proportion of fine particles in the sediments has been accompanied by important changes in the fauna of the bottom.

Quantitative Study of the Burrowing Animals

The disappearance of the eel grass around Woods Hole may have had both direct and indirect effects. Directly, it has brought a loss of feeding grounds, shelter, and support, and in these aspects it has not been replaced. Indirectly, the disappearance of the plant may have caused changes in the water circulation in the lagoon, changes in the amount of dissolved oxygen, in temperature, and in pH. The relative importance of the physico-chemical changes com-

TABLE I. *Showing the relative abundance of characteristic species in the N. W. Gutter lagoon before and after the disappearance of the eel grass* [3]

I. Animals formerly growing on the plants	Occurrence	
	Before	After
Coelenterata:		
Sagartia luciae	* [4]	
Bryozoa:		
Bugula turrita	***	
Arthropoda:		
Idothea baltica	*	
Mollusca:		
Bittium alternatum	**	
Lacuna vincta	**	
Littorina sp.	***	**
Mitrella lunata	*	
Total number of characteristic epiphytic species	7	1
II. Animals formerly swimming among the plants		
Annelida:		
Podarke obscura	*	
Arthropoda:		
Crago septemspinosus	*	*
Gammarus sp.	**	**
Palaemonetes vulgaris	**	**
Virbius zostericola	**	
Mollusca:		
Pecten irradians	**	
Total number of characteristic swimming species	6	3
III. Animals living on the surface of the mud		
Coelenterata:		
Hydractinia echinata [5]	**	**
Arthropoda:		
Carcinides maenas	**	
Libinia dubia	*	
Libinia emarginata	*	*
Pagurus longicarpus	***	***
Pagurus pollicaris	*	*
Neopanope texana sayi	**	**
Limulus polyphemus	**	*
Mollusca:		
Crepidula convexa	**	**
Crepidula fornicata	*	*
Crepidula plana	**	*

III. Mud-surface forms (continued)	Occurrence	
	Before	After
Nassa obsoleta	***	**
Nassa trivittata	**	**
Modiolus demissus	***	
Mytilus edulis	**	
Ostraea virginica	*	*
Total number of characteristic mud surface species	16	12
IV. Burrowing forms		
Nemertea:		
Cerebratulus lacteus	*	*
Micrura leidyi	***	
Echinodermata:		
Leptosynapta inhaerens	***	*
Thyone briareus	***	**
Annelida:		
Amphitrite ornata	**	*
Arabella opalina	**	**
Cistenides gouldi	**	**
Clymenella torquata	**	***
Diopatra cuprea	*	
Glycera sp.	***	*
Lumbrinereis tenuis	*	***
Maldane urceolata	*	*
Nereis virens	***	
Scoloplos fragilis	***	***
Spio setosa	*	***
Phascolosoma gouldi	*	*
Arthropoda:		
Pinnixia chaetopterana	*	*
Mollusca:		
Cumingia tellinoides	**	
Ensis directus	*	*
Mactra lateralis	*	*
Mya arenaria	***	*
Solemya velum	**	
Tellina tenera	**	**
Venus mercenaria	**	**
Chordata:		
Dolichoglossus kowalevskyi	*	*
Total number of characteristic burrowing species	25	20
Grand total of characteristic species	55	36

[3] Allee ('23a) lists 138 species found in the eel grass areas from 1915 to 1921. Of these, 18 species were never found in the N. W. Gutter and 64 species were so rarely present there as to be found only during one or two years, or else were so scarce in number as to be found by only one or two collecting parties a year; these very rare species have been considered unimportant in the population as a whole and have therefore been omitted from this list for the sake of clarity.

[4] * Occasional: Before—found in less than 33 per cent of Allee's collections. After—forming less than 2 per cent of the 1936 population.

** Common: Before—in 33 per cent to 50 per cent of Allee's collections. After—forming 2 per cent to 5 per cent of total population.

*** Abundant: Before—in over 50 per cent of Allee's collections. After—forming 5 per cent or more of the total population.

[5] Since the hermit crabs, on whose shells this hydroid lives, are to be found on the surface of the mud, this seems the best place to classify Hydractinia.

pared to the biotic changes remains to be investigated, but Prenant's study suggests that the direct effects are probably the major ones at Woods Hole as well as in Brittany.

The change brought the burrowing forms into prominence, and a census of these was made. At low tide, samples were collected at ten different points in the lagoon, then under 15 to 45 cms. of water. A unit area of 0.1 sq. meter was inclosed by a sheet iron frame 20 cms. wide and 50 cms. long. All the sediment within the frame to a depth of 30 to 40 cms. was shoveled out and placed in buckets until it could be sieved. All specimens retained by the 3½ mm. mesh were saved, identified, and counted. About 275 individuals of 23 species formed the population of one square meter. Table II lists the species found, and their abundance.

TABLE II. *Abundance of 23 species at various stations*

Species	Total number animals	No. of stations where found	Stations								
			1	2	3	4+5	6	7	8	9	10
Scoloplos fragilis	86	10	1	5	11	19	2	15	17	4	12
Clymenella torquata	52	8	3	16	5	24	1	0	0	1	2
Lumbrinereis tenuis	41	8	1	8	6	11	7	0	2	6	0
Spio setosa	23	8	0	7	9	3	1	1	1	1	0
Tellina tenera	16	6	3	0	1	1	4	0	0	3	4
Cistenides gouldi	14	7	0	1	6	3	0	1	0	2	1
Nassa trivittata	10	5	6	1	1	0	1	0	0	1	0
Mactra lateralis	8	5	0	1	1	0	2	2	2	0	0
Venus mercenaria	5	3	1	0	0	0	3	0	0	1	0
Arabella opalina	4	3	0	2	0	0	1	0	1	0	0
Pinnixia chaetopterana	5	2	0	0	0	3	0	0	0	2	0
Maldane urceolata	3	2	0	2	0	1	0	0	0	0	0
Cumingia tellinoides	2	2	0	0	0	0	0	0	0	1	1
Amphitrite ornata	2	2	0	0	0	1	0	0	0	1	0
Glycera americana	2	2	0	1	1	0	0	0	0	0	0
Mya arenaria	2	2	0	0	1	0	1	0	0	0	0
Dolichoglossus kowalevskyi	2	1	2	0	0	0	0	0	0	0	0
Cerebratulus lacteus	1	1	0	0	0	1	0	0	0	0	0
Ensis directus	1	1	0	0	0	1	0	0	0	0	0
Lyonsia hyalina	1	1	0	0	0	0	0	0	0	1	0
Haminea solitaria	1	1	0	0	0	0	0	0	0	1	0
Phascolosoma gouldi	1	1	1	0	0	0	0	0	0	0	0
Unicola irrorata	1	1	0	0	0	1	0	0	0	0	0
Total	273										

I am indebted to Dr. A. C. Redfield for advice on this study, to Dr. W. C. Allee for suggestions and for approval of my interpretation of the condition of the eel grass community as he studied it, and to Mr. G. M. Gray for several of the identifications.

SUMMARY

A comparison has been made between the animal communities of a typical eel grass area before and after the almost complete extermination of the

plants by a mycetozoan parasite. The data came from Allee's papers on the animal communities of Woods Hole and from my observations and quantitative survey of the burrowing animals of the area. As might be expected, practically all the animals once found living on or among the eel grass disappeared with it, and although the total number of burrowing species fell slightly, they now constitute a much larger proportion of the population than formerly. The decrease in complexity of environmental conditions due to the disappearance of the vegetation has been accompanied by a decrease in the number of characteristic species from 55 to 36, a loss of one third, and no new species have been noted.

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Contribution No. 135

The Biology of the Zooplankton Population in the Bay of Fundy and Gulf of Maine with Special Reference to Production and Distribution.

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and
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(*Contribution No. 135 of the Woods Hole Oceanographic Institution*)

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ABSTRACT

Analyses in the gulf of Maine and bay of Fundy show the zooplankton population to be dominated by a relatively few species of boreal endemic crustaceans. *Calanus finmarchicus,* the most abundant form, averaged 39.9 per cent by number in the total region during the period, April to September in 1932, and 35.5 per cent for the year in the bay of Fundy. Fluctuations in the volume of zooplankton reflect to a large extent numerical changes in the stock of this species. The vernal rise in 1932 occurred following propagation of *Calanus,* and the rapid downward trend in June coincided with the critical period of maturation and subsequent mortality of adults after spawning.

Due to differences in the time of spawning in different parts of the region, two, and in some cases three, breeding stocks of boreal plankton animals can usually be distinguished. The distinct spawning periods are continued in subsequent generations that year no matter where distributed.

Productivity was found to be closely correlated with temperature and stability of the water mass, and dispersal with the nontidal circulation in the region. The vernal crop of boreal plankton species appears to be derived largely from adults maturing in the western or outer gulf. With the advance of the season the centre of production moves to the eastern basin. The turbulent New Brunswick-eastern Maine coastal zone as far west as Mount Desert is relatively unproductive, and characterized by small zooplankton volumes.

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PREFACE

The present report on an investigation covering the period July 28, 1931 to September 29, 1932 forms part of the program of the International Passamaquoddy Fisheries Commission. This paper has been prepared by the senior author, who assumes responsibility for the opinions and conclusions presented. The junior author rendered valuable assistance in field work and laboratory analyses during the investigations of the second year. Reports have already appeared on phytoplankton by Dr. H. H. Gran and Mr. Trygve Braarud (1935), herring by Mr. Michael Graham (1936), hydrography by Dr. E. E. Watson (1936) and the biologies of three species of copepods, *Calanus finmarchicus, Pseudocalanus minutus,* and *Oithona similis,* by Dr. C. J. Fish (1936a, 1936b, 1936c).

We desire to express thanks to Dr. A. G. Huntsman and Dr. H. B. Bigelow for many helpful suggestions and the facilities of the Atlantic Biological Station and the Woods Hole Oceanographic Institution. Acknowledgment is also made to our above mentioned colleagues, for generous co-operation at all times, to Mr. W. Herrington, Mr. H. B. Hachey, Dr. A. H. Leim and Mr. O. E. Sette for valuable material and information, and to Miss H. E. Rigby, clerk, for assistance in computing results.

INTRODUCTION

The problem confronting the Commission has been to determine to what extent the fishery of the Quoddy region would be affected, favourably or unfavourably, by the construction of a series of hydroelectric power dams in the entering passages to Passamaquoddy bay, situated on the boundary between Maine and New Brunswick. The zooplankton aspect of this problem is concerned with the influence of the mixing mechanism in the passages on the production and availability of food for plankton-feeding fishes, particularly of the herring which forms the most important commercial species in the region.

A theory had previously been advanced (Huntsman 1928, p. 34) that the thorough tidal mixing of the water mass results in an indraft of deep water, rich in plankton animals, which provides an abundant supply of available food, and this might account at least in part for the large herring population (Graham 1936, p. 125). Although this condition is attributed only to the zone of mixing, it presupposes an abundant source of zooplankton supply in the deep layers of the immediate area outside of the passages. In addition to the evidence offered by the fishery this viewpoint is supported by large flocks of sea birds which collect in the region of the most violent mixing during the summer, and also by frequent swarms of *Meganyctiphanes norvegica* observed commonly here and rarely elsewhere at the surface.

Contrasted with these indications of an abundant zooplankton supply are records of consistently scanty hauls made by previous investigators in this area (Bigelow 1914a, pp. 34, 104 and 130; 1926, pp. 83-85), and evidence that propagation of some of the important species of the year-round population is largely

unsuccessful in the bay of Fundy (Huntsman 1918, p. 65; Huntsman and Reid 1921, p. 110; Wright 1929; Battle 1930).

It had further been suggested that the influence of Quoddy mixing is not purely local, but through the agency of ocean circulation nutrient salts are transported out of the region. Mixed water leaving the Quoddy region would be expected to move out of the bay of Fundy along the east side of Grand Manan and thence in part to the coast of Maine, to supplement the results of local mixing (Huntsman 1928, p. 35).

The problem therefore necessitated a consideration of the zooplankton population of the general region which might serve as a source of supply for the Quoddy area or be influenced by outwash from it. Essentials to be determined were: (1) the quantity of zooplankton, (2) its composition, (3) source and dispersal, (4) the extent to which the stock in the bay of Fundy (including Passamaquoddy bay) is recruited from breeding areas within and beyond the influence of Quoddy mixing, and (5) possible correlation of zooplankton with herring concentration in the Quoddy region.

Program and Observations

Field operations

Field work began on July 28, 1931, and during the first summer was confined to local studies in the Quoddy area, with the exception of one cruise (no. 4) along the coast of Maine as far west as Casco bay on August 21 to 26, and another (no. 5) in the bay of Fundy as far east as cape Spencer on September 1 to 5 (fig. 1).

Throughout the autumn and winter of 1931-32, four stations (sta. 1C, 5, 6, and 8A) were taken at regular intervals to indicate seasonal changes in the zooplankton of Passamaquoddy bay, the Outer Quoddy region, and two offshore localities in the bay of Fundy (cruises 6-25). These routine observations were supplemented during December and January by 49 Petersen trawl samples taken in the course of herring investigations by Mr. M. Graham over a wide area in the bay of Fundy and extending south of cape Sable. Although highly selective and not comparable with metre net collections for quantitative studies, they indicate the distribution of larger members of the zooplankton population, particularly the euphausiids and sagittae. Unfortunately, due to a fire, no data are available for the period between January and March, 1932.

Beginning April 15, 1932, monthly cruises were instituted, covering a series of 28 stations located in eight sections between cape Spencer and Casco bay (fig. 2). These cruises, covering the spring and summer propagation periods, occurred as follows: cruise 26, April 15-May 2; cruise 27, May 19-31; cruise 28, June 20-July 1; cruise 30, August 8-21; cruise 32, September 14-26.

At times during the second season it was possible to enlarge the range of observations through co-operation with vessels operating simultaneously in other parts of the region. In April the zooplankton material was supplemented by a series of half metre net collections from the vicinity of Georges bank (fig. 2, Albatross stations) and a double line of observations (half metre net and Petersen

trawl) along the coast from Passamaquoddy bay to Halifax (Nova series). In May, collections (metre net) were obtained from a line of eight Nova stations between cape Sable and cape Ann and eight stations in the bay of Fundy. In August a series of 16 special stations was made in inland waters extending from Casco bay, Maine, to Maces bay, New Brunswick, with two on the Nova Scotian side in St. Mary bay and Annapolis basin (fig. 2). Eleven special stations (Atlantis series) widely distributed over the gulf of Maine and Georges bank were made in September.

Between the monthly cruises observations were restricted to the Quoddy region, cruise 29 (July 30) comprising stations 1C and 5 (fig. 2), and cruise 31 (September 12-13), a series of simultaneous collections in the Western passage, the Letite passages, and adjacent waters on various phases of the tide for the purpose of determining the extent of zooplankton interchange between Passamaquoddy bay and the Outer Quoddy region.

FIGURE 1. Zooplankton stations in 1931.

ZOOPLANKTON MATERIAL

Quantitative and qualitative analyses were made of 434 metre net, 107 half-metre net, 91 Petersen trawl and 174 pump samples. A series of 32 metre net samples taken in 1917 at Prince stations 3 and 5 in the bay of Fundy and station 6 in Passamaquoddy bay were also examined for purposes of comparison.

METHODS

Hydrographic determinations in connection with the zooplankton investigations were made with the same equipment and methods described in the report of the hydrographer (Watson 1936, p. 143).

The zooplankton field work consisted of an investigation of (1) breeding

areas, development and subsequent dispersal of young stages, and (2) quantitative and qualitative distribution (geographical and seasonal) of the adult population. Both of these lines of investigation were carried on simultaneously but with different methods.

For the sampling of eggs and immature stages, the pump was used during the summer months (July-September). A two-inch (ca. 5 cm.) rubber hose with a check valve near the end was attached to the dredging wire and lowered to the proper depths indicated on the metre wheel. With a double action hand pump equipped with a gauge, water was pumped into a plankton net (no. 20 silk) sus-

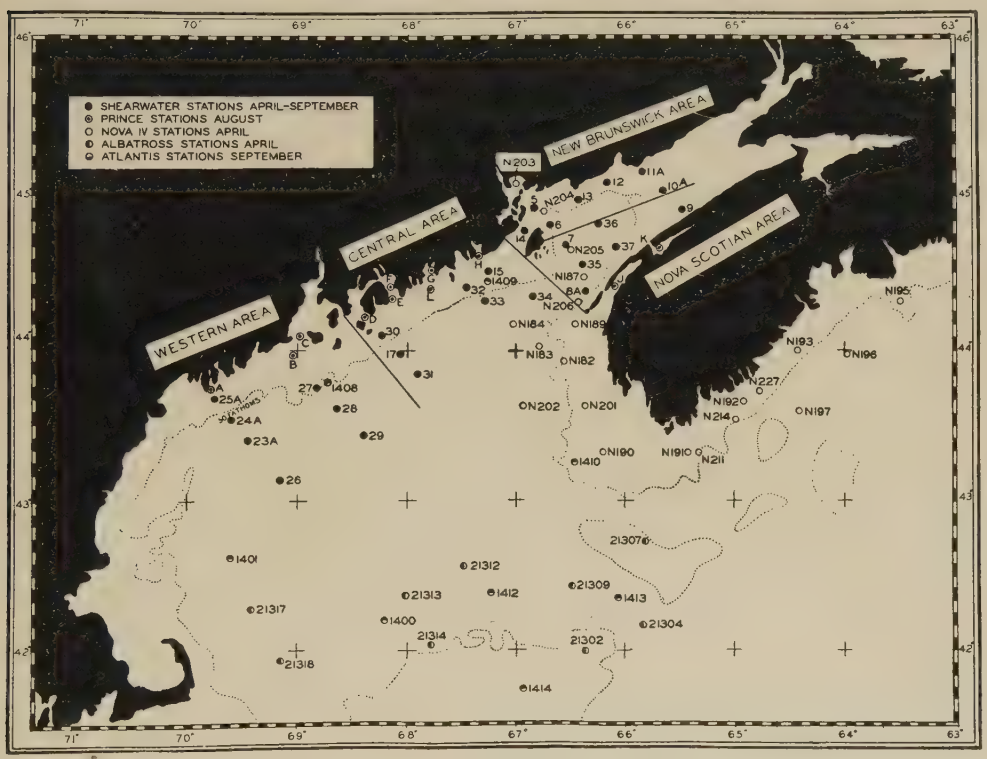

FIGURE 2. Zooplankton stations in 1932.

pended in a cylindrical tank. By raising or lowering the end of an overflow pipe attached near the bottom of the tank, it was possible o maintain the level of the water slightly below the mouth of the net, thus allowing maximum filtering surface without danger of crushing delicate organisms. The sample was removed from a petcock bucket at the cod end of the net, a volume of 250 litres of water from each of four levels, 0, 10, 30, and 50 metres being filtered at each station. Analyses were made by the Sedgewick-Rafter counting method, and the number of individuals per cubic metre calculated. A Stempel pipette was used in removing one cubic centimetre of the sample for counting. In determining horizontal distribution, the value taken for each station represents the mean of the four levels.

Until weather conditions permitted the use of the pump (end of June) half-metre nets (two metres in length) of no. 10 silk were utilized. The hauls were of 15 minutes duration and were oblique from 50 metres to the surface. The counts were made as in the pump samples, except that the number of organisms per minute of towing was taken as the unit of measure.

For adult population studies metre nets of the standard type used by the U.S. Bureau of Fisheries were selected. These were one metre in diameter and four metres long. The first metre, forming the cylindrical section, was of no. 0000XX and the remaining conical portion of no. 0XX bolting silk.

From July, 1931, until April, 1932, the collections were made by horizontal hauls of 20 minute duration at the surface, 50 metres, and as near as possible to the bottom. In depths not exceeding 60 metres only two hauls were made. Subsurface collections in all cases were made with closing nets.

Oblique closing net hauls were substituted in place of horizontal towing during the second season (cruises 26-32). These consisted of a lower haul from near the bottom to 50 metres where the net was closed, and a second haul from 50 metres to the surface. Horizontal haul volumes were measured by the settling method and oblique hauls by both settling and displacement methods, the time interval of the haul being used as a unit of measure.

The qualitative analyses of metre net collections were made in the following manner: after the volume of the sample had been determined it was thoroughly mixed and a portion removed with a Stempel pipette (2 cc.) and transferred to a petri dish for counting. If the specimens were large, four and sometimes six cubic centimetres were removed. Counting was done with the lowest magnification possible for accurate identification, and varied according to the nature of the sample. In each sample the total number of all species occurring in five fields of the microscope were counted, totalled, and their *relative percentage by number* computed. The remainder of the sample was then examined and any species not included in the counts listed as traces (T). In the present report, unless otherwise stated, the percentage value assigned to each species will represent the mean based on collections from all depths.

Collecting by other vessels was done with equipment supplied by the Commission and with uniform methods. Petersen trawl collections were made in oblique hauls from the bottom to the surface.

To record repeated observations at the same stations, the cruise number was inserted before the station number, the two being separated by a decimal point, as 05.06 indicating cruise 5, station 6. For special stations made possible through co-operation with other investigators, their numerical series have been inserted with the name of the ship. Where changes in the location of regular stations were made, the new position is indicated by the former station number with a letter added, as in the case of sta. 8A. A series of neritic stations in August, 1932, were assigned alphabetical letters.

PHYSICAL OBSERVATIONS

The production, dispersal, and survival of zooplankton populations are more closely correlated with hydrographic conditions than with any other readily detectable controlling factors. Temperature appears to determine largely the type of community which can maintain itself in any particular area, while depth, circulation, turbulence, and, in extreme cases, salinity influence, its horizontal distribution.

In summarizing physical characteristics and seasonal changes in the region, it has been necessary to draw largely upon the results of previous investigators. For a more detailed account of the hydrography of the bay of Fundy during the period of the present investigations see Watson (1936), and for vertical profiles of temperature and salinity correlated with phytoplankton and chemical data, Gran and Braarud (1935). It will be our purpose here to consider only those aspects which appear to be of particular significance in the biology of zooplankton.

Temperature

The gulf of Maine is at the surface an open bay. Between 10 and 50 metres, Georges bank forms an island approximately 100 miles long (at the latter level) across the entrance, and the point of Nova Scotia extends about 40 miles farther west than at the surface. Below the 100 metre level the gulf is an almost enclosed basin with two narrow entering passages.

Separated from the open Atlantic by topographical and hydrographical barriers, temperature variations are for the most part indicative of local response to seasonal changes. External influence, sufficient to affect significantly biological conditions, originates from three principal sources: (1) an inflow of warm (6° to 8°C.) slope water through the eastern channel along the bottom, particularly in the spring, maintains a uniform bottom layer of approximately 5° to 6° in the deeper parts of the gulf throughout the year (winter cooling penetrates to depths of less than 150 metres); (2) an inflow of cold water in the upper 100 metres past cape Sable from the eastward in late March and April is variable, but temporarily retards and may even reverse vernal warming of the surface layer in the northeastern part of the gulf, sometimes lowering it to 0°; (3) an outwash of cold water from the Saint John river with the melting of the ice for a short time exerts a somewhat similar influence over a smaller area in the bay of Fundy, at first retarding vernal warming of the surface stratum and later resulting in a localized band of cold water (4° to 6°) which follows the course of the drift at an intermediate level along the New Brunswick coast and remains against the eastern slope of Grand Manan through the greater part of the summer.

ANNUAL TEMPERATURE CYCLE

The region can be classed as typically boreal, having an average offshore range over the gulf from about 2° to 20°C. and in the bay from 1° to 15°C. The Nova Scotian current may lower temperatures temporarily to 0°C, in the northeastern part of the gulf, and the Saint John outwash to 0°C. or even lower in the bay. A

zooplankton population concentrated by day below 40 metres would, throughout the region, encounter there an annual variation of not more than 10° and in the deeper levels (below 150 metres) probably less than 4°.

In the gulf of Maine autumnal cooling becomes noticeable first in August or early September in the more stratified western and deeper areas where the summer maximum may be passed a month earlier than in the more turbulent region east of Penobscot bay. At depths of 100 metres warming may continue into December. Vernal warming begins at the surface in late February or early March. At this time the water mass is heated both from above and below, the latter due to bottom

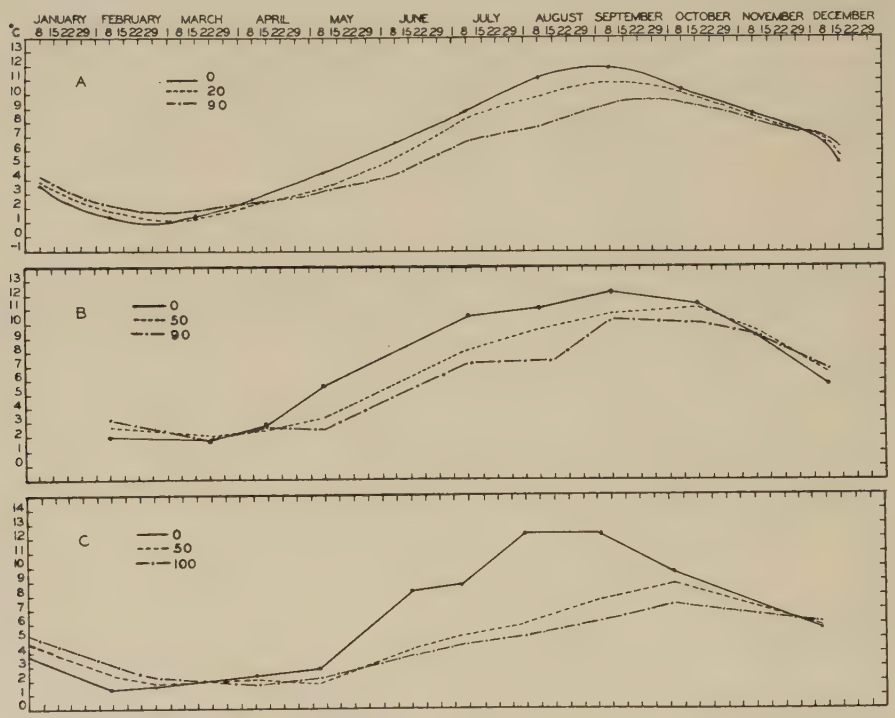

FIGURE 3. Average range of temperature at station 5 during the period 1921-1930 (A), and in 1932 (B); station 6 (Prince sta. 3) in 1917 (C). Monthly readings. Depth in metres.

slope water mixing with the adjacent colder layer above. Bigelow (1927, p. 546) estimates that "during the first weeks in March the warming affected from below by this source raises the temperature of the deep waters of the inner part of the gulf as rapidly as solar heat warms the surface stratum". By the end of April warming from above has penetrated to a depth of 100 metres in the western side of the basin and in the northeastern side from below to within 15 to 20 metres of the surface (Bigelow 1927, p. 547). The water mass becomes highly stratified over much of the gulf during the summer, the surface layer reaching at times 20°C. or more in the western basin. Relatively low surface temperatures due to turbulence prevail throughout the summer in the eastern coastal area, the cape Sable region and on the offshore banks.

In the bay of Fundy the surface begins to cool early in September and in the more turbulent areas is soon followed by a decline in the lower levels. However, cooling does not become appreciable until considerably later than in the gulf. In deeper, more stable areas (fig. 3) heating of the lower strata may continue into October. The whole water mass reaches a uniform temperature of 6.5° to 7.5°C. in November, and with continued cooling remains substantially the same from top to bottom until April. Minimum values of 1° to 1.5°C. are found at the surface in February or early March.

With a slight warming at the surface in March the water mass again becomes homogeneous at approximately 2°. The increase in surface temperatures varies greatly in different parts of the bay, depending on the intensity of mixing. In the more stable areas (fig. 3A) the upper stratum warms more rapidly and reaches its maximum earlier in the season than in turbulent areas like the Quoddy region (fig. 3B) where the absorbed heat is distributed over a much wider vertical range. The entire Fundy region, however, is subjected to such violent tidal action that temperatures over the greater part of the bay do not usually rise above 12°C.,

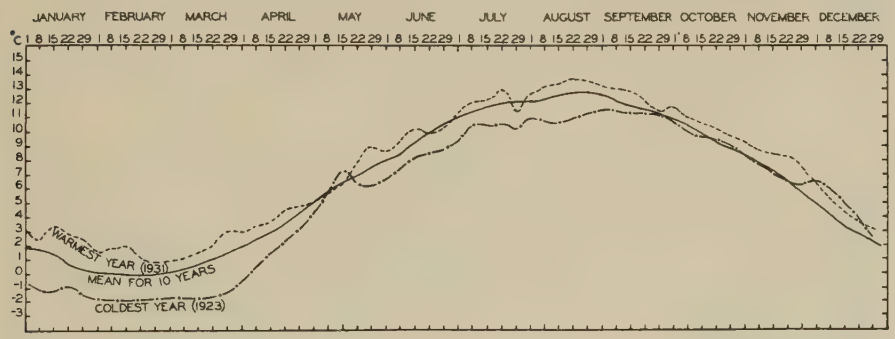

FIGURE 4. Average range of temperature at St. Andrews during the period 1922-1931, and in the coldest (1923) and warmest (1931) years. Based on daily readings.

and, although there is considerable regional variation (Bigelow 1927, p. 591), higher offshore values, when they occur, can have little biological significance, being too restricted in area and of short duration. The maximum temperature (15.13°C.) in 1932 was recorded on August 19.

Of importance to the biologist seeking causes for fluctuations in animal populations is the apparent slight variation in the temperature cycle from year to year in any one locality. This has previously been noted by Bigelow (1927, p. 628) who states, "More or less fluctuation in summer temperature is to be expected in any partially enclosed basin as subject to violent climatic changes as is the gulf of Maine, and where waters of different temperatures meet. What really deserves emphasis is that the yearly changes have been very small during the period of record; certainly not enough to seriously affect the waters of the Gulf as a biologic environment, except perhaps in 1916."

Even in shallow inshore waters affected by ice conditions, and more readily

responding to low air temperatures, the fluctuations are surprisingly small. The warmest (1931) and coldest (1923) years recorded for the period 1922-1931 at St. Andrews, New Brunswick (fig. 4), show a deviation of less than 3°C. above or below the mean. It is improbable that high temperatures, usually of short duration, ever prove fatal to the *neritic* population, but unusually low temperatures over an extended period such as those prevailing at St. Andrews from January

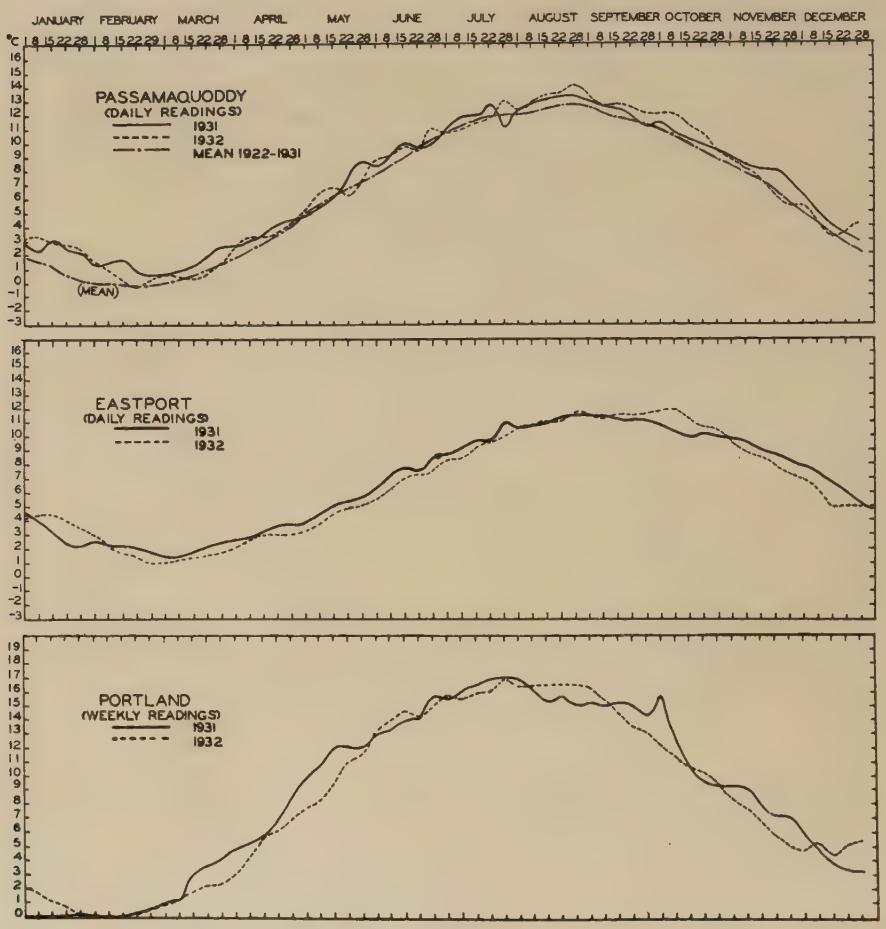

FIGURE 5. Annual range of temperature in 1931 and 1932 at St. Andrews, Eastport and Portland.

to the end of March in 1923 (–1° to –2°C.) no doubt prove destructive to certain members of the benthonic community which in boreal waters appear to have a minimum temperature limit very close to that usually found in their particular locality. In the gulf this would be expected to be approximately 0° to 1°C.

The surface temperature data for St. Andrews indicates that 1931 and 1932 were "warm" years and for the greater part of the year slightly exceeded the mean, especially during late winter and mid-summer. (fig. 5). It was not possible

to construct a mean range for other localities, but the surface temperature records for both Eastport and Portland coincide closely for 1931 and 1932.

Bays in the western part of the gulf appear to respond more quickly to autumnal cooling, and vernal warming, and decline in temperature almost as much as those farther east in more tide swept areas. It is interesting to note that in

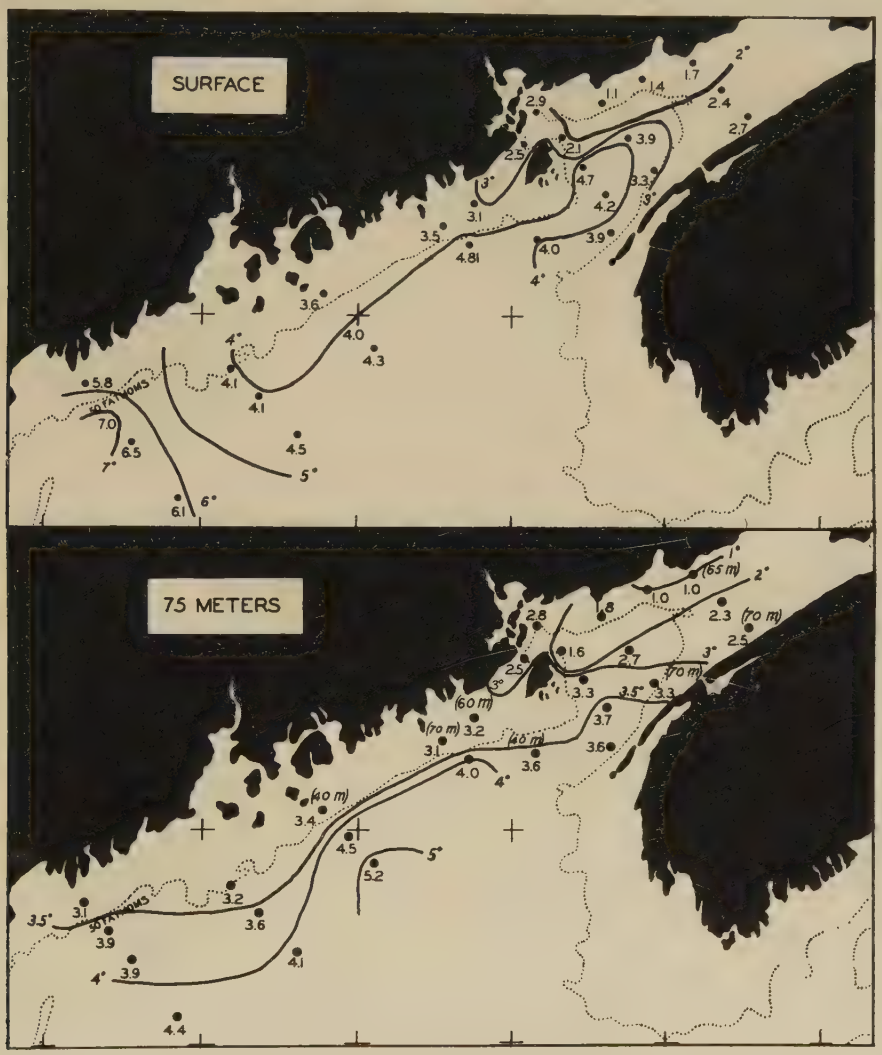

FIGURE 6. Temperature in April, 1932.

1931 surface temperatures at Portland were lower than at St. Andrews throughout the coldest months, January and February. In 1932 a temperature of 1°C. was reached at Portland on January 16, and 0°C. on January 28. The water did not rise above 0°C. until February 23, reaching 2°C. on March 18 and 3°C. by the end of the month. At St. Andrews the temperature did not fall below 1°C. until

February 5, and reached zero only on March 17 at a time when the temperature at Portland had risen 2°C. above the winter minimum. Warming was slower throughout the spring in Passamaquoddy bay, and the temperature did not rise above 2°C. until the end of March. The response in 1932 thus appeared to be about two weeks later at St. Andrews than at Portland during late winter and early spring. The maximum temperature recorded in 1932 at the latter point was 17°C. on July 29-30, and at the former, 14.3°C. on August 30.

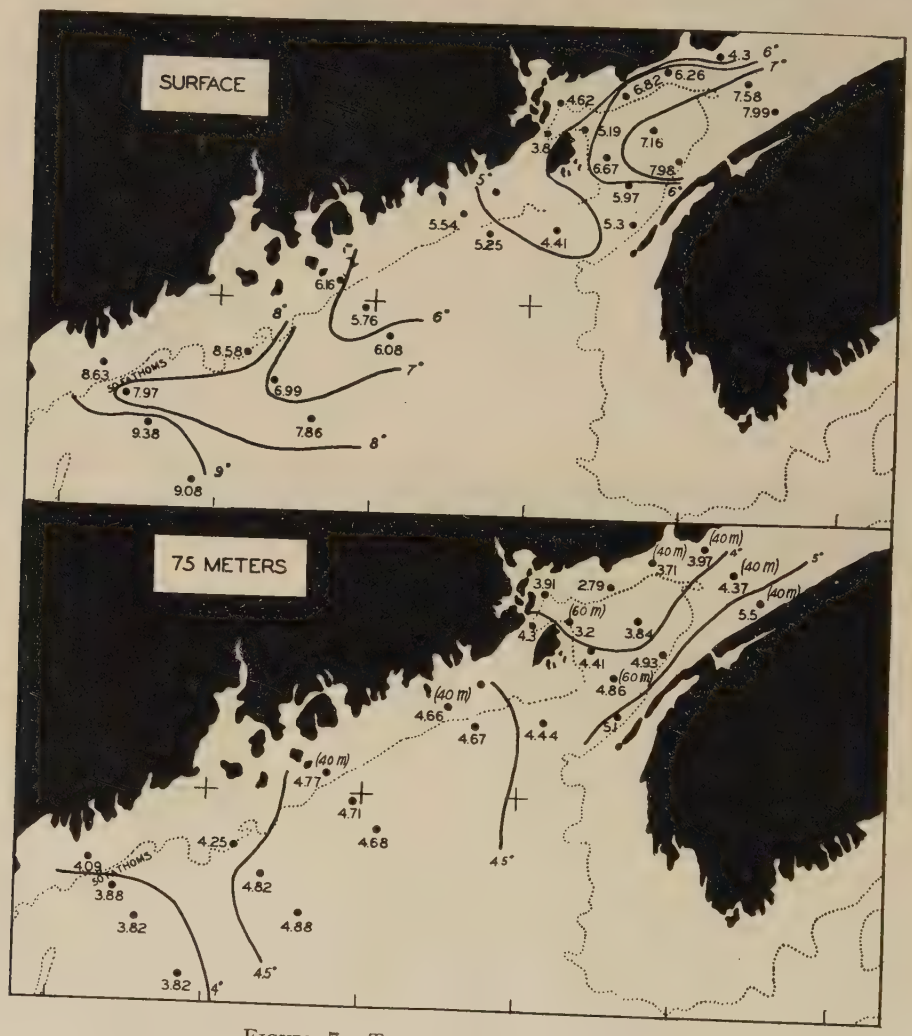

FIGURE 7. Temperature in May, 1932.

HORIZONTAL DISTRIBUTION OF TEMPERATURE IN 1932

For present purposes, the horizontal distribution of high temperatures, low temperatures and relatively homogeneous water, particularly during the periods of restocking, appears to be of greatest biological importance (pp. 310-312). The

present data from April until September (1932) accord so closely with the published records for previous years (Bigelow 1917, 1922 and 1927) that only a brief summary with figures showing seasonal changes will be presented at this time.

When investigations began in late April (cruise 26) the western area had warmed to from 5° to 7°C. (fig. 6), but over the remainder of the gulf and central

FIGURE 8. Temperature in June, 1932.

basin in the bay surface temperatures ranged from 3° to 4.8°C. The coldest surface water was found along the New Brunswick coast (1.1°C.) influenced by the Saint John outwash. The relative distribution of temperatures at 75 metres (fig. 6) was much the same as at the surface, except that the influence of slope water was detectable at the deepest station off Mount Desert Island.

In May (cruise 27) the upper stratum warmed to at least 5°C. everywhere

except off Saint John, the Quoddy region, and station 34 near Grand Manan bank. West of Mount Desert temperatures ranged from 6° to 9.08°C., and in the more stratified parts of the bay from 6° to 7.99°C. The effect of the cold Nova Scotian current is indicated by a cold band of less than 6°C. extending across the entrance to the bay of Fundy and reaching as far as Mount Desert. Its influence is further detectable in a tongue-like projection of all isotherms along the course of the drift at least as far west as Casco bay.

FIGURE 9 (part)

By June (cruise 28) the temperature in the western area exceeded 15°C. decreasing gradually to 10°C. off Penobscot bay, and 7° to 8°C. east of Mount Desert. The coldest surface water (6.14° to 6.95°C.) was found in the Quoddy region and Grand Manan channel. East of Grand Manan temperatures from 8°

to 9.5°C. occurred over the central basin but the greater part of the bay was below 8°C. Below 40 metres the western area after June was coldest, and the bay of Fundy, including the eastern coastal region of the gulf, warmest.

Surface temperatures over the greater part of the gulf ranged from 15° to 19°C. in August, and in the bay from 12° to 14°C. with very localized areas of 10.48° to 15.13°C. (fig. 9). Mixing, indicated by low surface temperatures (9.3° to 11°C.), was most pronounced at this time in the northeastern part of the gulf

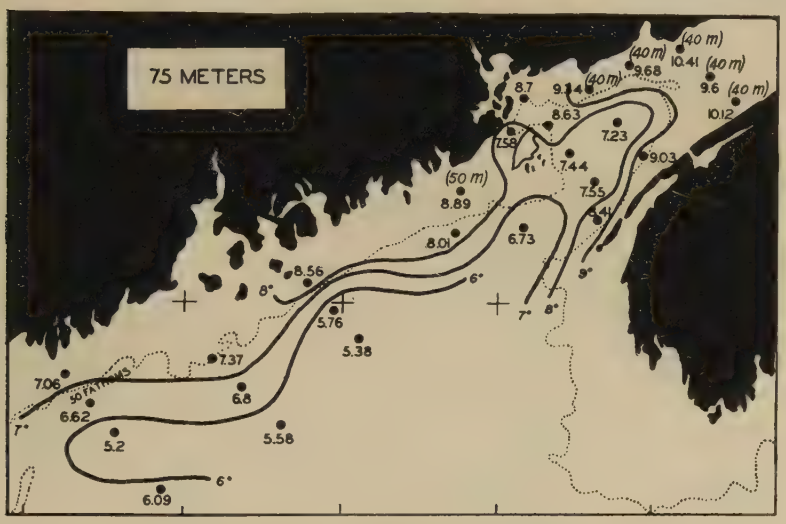

FIGURE 9 (con.) Temperature in August, 1932.

between Petit Manan and Grand Manan, with water of less than 13°C. extending west of Penobscot bay. Temperatures below 7°C. were now restricted to the gulf within the 100 metre contour.

Autumnal cooling had reduced temperatures over the greater part of the gulf by the middle of September (fig. 10). East of Mount Desert to the Quoddy region there had been a slight increase, but elsewhere in the bay of Fundy, due perhaps more to violent mixing at the entrance than to seasonal cooling, surface temperatures, particularly on the Nova Scotian side, had declined from the August maximum. The lowest surface reading was 9.6°C. off Briar Island (sta. 8A).

CIRCULATION

For additional data on the direction and rate of dispersal of eggs and larvae during the important augmentation period in May and June (1932), drift bottles were set out along the lines of zooplankton stations in the gulf of Maine and bay of Fundy. The bottles were of the type used by the U.S. Bureau of Fisheries and equipped with a two-metre drag to reduce wind action. Of 446 liberated 106 have been recovered. (See table II, pp. 214-217.) The probable courses taken by these bottles have been plotted to accord with other hydrographic evidence and with the findings of previous investigators.

The non-tidal circulation in the gulf of Maine is counter clockwise eddying about a central vortex, the location of which varies from off the bay of Fundy to a point from 60 to 70 miles south of Mount Desert island (Bigelow 1927, p. 972). There is some seasonal and annual variation, but the general movement about the gulf is continuous throughout the year. Inflow at the surface is most evident at the eastern side of the gulf, and outflow at the western, past cape Cod, with some discharge around the eastern end of Georges bank. As previously stated, bottom water enters through the eastern channel.

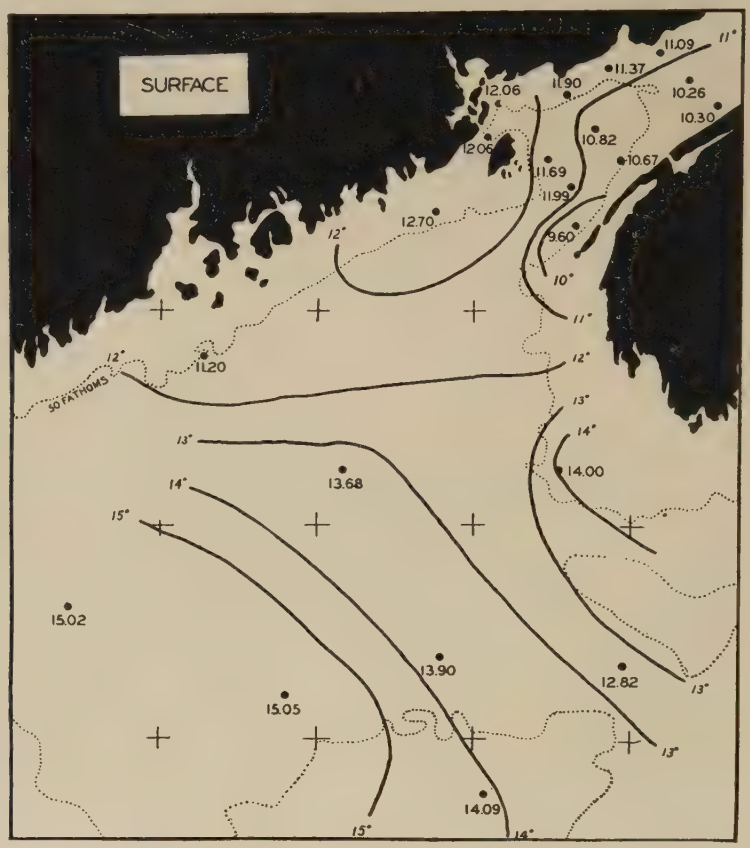

FIGURE 10 (part)

In the inner part of the gulf, west of Mount Desert, the general movement during the summer of 1932 was offshore except close to the islands where drift bottles indicated an along-shore set (series C and D, western part). East of Mount Desert to Grand Manan the general circulatory drift is complicated by the topography and local hydrographical conditions which appear to retard any dominant westerly movement in that sector. This is suggested by the relatively long interval of time before bottles set out in this area were recovered, and also by the zooplankton in which the horizontal variation was more marked than would

be expected along the course of a continuous drift. From the small number of bottles grounding in this area the dominant set would appear to be offshore as far east as Machias, except for a westerly set close to the land. Bigelow's drift bottle results suggest that ". . . such parts of the dominant surface drift as veers westward past Grand Manan does not usually strike the coast of Maine in summer until it has passed the longitude of Mount Desert," (Bigelow 1927, p. 907).

After circling the outer part of the gulf a portion of the drift completes the circuit across the entrance of the bay of Fundy and west along the coast of Maine.

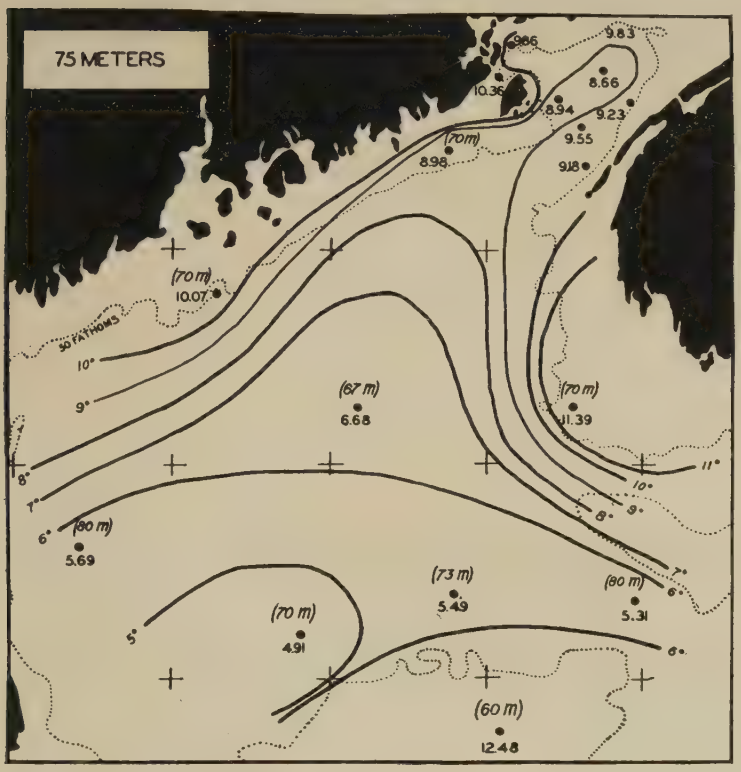

FIGURE 10 (con.) Temperature in September, 1932.

A branch constituting, according to Bigelow's records (1927, p. 906), the greater volume, continues east into the bay on the Nova Scotian side. Bigelow (1927, p. 972) found that "This Nova Scotian side of the gulf of Maine eddy also receives water in some volume from the dead zone off cape Sable in summer, and in some years a westerly drift past cape Sable into the gulf of Maine persists from spring through summer." Close to the southern shore the indraft into the bay of Fundy extends to the headwaters, but the major portion follows the 100-metre contour to form a second (counter clockwise) eddy whose outer margin does not extend far beyond the slope of the basin. It passes west along the New Brunswick coast and out of the bay along the eastern and southern sides of Grand Manan where

it becomes a part of another (clockwise) eddy movement having Grand Manan as a vortex. This latter eddy was suggested by Bigelow (1927, p. 973) who described an eastward drift along the southern shore in Grand Manan channel

FIGURE 11 (part)

(Mavor 1922; Watson 1936), a movement involving, however, only a small part of the water leaving the bay—the major drift appears to be west to the coast of Maine.

The Quoddy region and the Grand Manan channel lie out of the main course of the Fundy drift and form a sort of pocket in which biological interchange with outer waters is apparently relatively slow. Surface waters entering the region

FIGURE 11 (con.). Assumed drifts of bottles recovered from series A-D, released in the gulf of Maine, May 24-30, 1932.

appear to be derived largely from the along-shore area to the east, relatively barren in zooplankton. Drift bottles showed little evidence of surface indraft from offshore except those set out in the immediate vicinity which moved into the

western passage, out through the Lubec narrows and west along the north shore of Grand Manan channel. But one bottle entered Passamaquoddy bay (fig. 13), apparently through one of the Letite passages.

The principal exchange of waters in the Quoddy region appears to involve an indraft of heavy bottom water through the channel between the Wolves bank and Grand Manan, and, after thorough mixing with light river water, an outflow at an intermediate level. This movement is not sufficiently active to be detectable in available biological evidence.

RATE OF DRIFT

Knowing the approximate rate of development of pelagic eggs and larvae (confined largely to the upper strata) taken at any point along the course of a known drift, as in the gulf of Maine, the velocity of the transporting current

FIGURE 12. Assumed drifts of bottles recovered from series H-J, released in the gulf of Maine on June 26-28, and in the Roseway bank region on July 16, 1932.

affords a means of estimating roughly the possible distance traversed and the probable source of supply. This method has previously been applied in the gulf of Maine in considering the dispersal of *Gadus callarias* eggs and larvae (Fish 1928 and Schroeder 1930).

The probable rate of drift in the region at certain seasons has been estimated by several investigators. In the bay of Fundy in May, 1930, Hachey's records indicated a minimum rate of four miles per day (1 mile equals 1.6 kilometres) around the circuit of the basin, and Mavor (1922, p. 16) during the late summer of 1919 reported a minimum velocity of four miles per day along the Nova Scotian shore and five miles per day along the coast of New Brunswick.

In the gulf drift bottles set out by Mavor in August travelled from the bay

of Fundy to cape Cod in 73 to 80 days at a rate of four miles per day (in a straight line). Along the outer course of the eddy, east from cape Ann, Bigelow (1927, p. 888) in August, 1923, found a velocity of three to four miles per day perhaps increasing to five or six miles near Nova Scotia. The quickest passage consumed 56 days, a rate of 4.7 miles along the assumed eddying route. Of three bottles set out off cape Ann in April, 1926 (Bigelow 1927, p. 878) two reached Digby county, Nova Scotia, in 73 and 77 days respectively, and one Lepreau harbour, New Brunswick, in 94 days.

Thus during the spring and summer, covering the most important periods of zooplankton production, the results of previous observers would indicate an average rate of about four miles per day about the periphery of the gulf and bay, perhaps increasing to five or more miles near the southern entrance to the bay and along the coast of New Brunswick, and rarely falling below three miles per day.

Bay of Fundy in 1932. In the bay of Fundy where the course of the set is fairly evident, drift bottle velocities in May and June, 1932, were found to accord very well with previous records. Figure 14A shows the points of liberation and recovery together with the interval of the drift of bottles found floating or probably obtained shortly after grounding. Three bottles set out south of Grand Manan on a line from the Wolves bank to Briar Island (series E) were found drifting along the New Brunswick coast between Saint John and Dipper harbour in 16 to 17 days, indicating a velocity of three and four tenths to four miles per day (bottles no. 106, 123, 136). Along the eastern side of Grand Manan the drift was more rapid, approximating five miles (bottle no. 84), and around the western margin of the eddy four to four and six tenths miles (bottles nos. 30, 89, 101). East of Digby gut the velocity of the set along the Nova Scotian coast was probably less than one mile per day, as the minimum interval of drift of bottles from the entrance to the vicinity of Minas basin was 82 days and the average 106 days.

Pelagic eggs and larvae entering from the gulf of Maine at this time would thus be expected to reach the New Brunswick coast in two to three weeks and might complete a circuit of the bay in from three to four weeks. Eggs produced along the north coast west of Saint John to Grand Manan could be transported beyond the confines of the bay in from one to two weeks, although a considerable proportion, particularly those produced within the 100 metre contour, might remain within the bay, following around the inner part of the eddy. One would look for the largest concentrations of zooplankton over the central basin in the vortex of the circuit.

Gulf of Maine in 1932. In the gulf, except in the case of the along-shore drift where the course of the set is evident, it is not possible to accurately determine the velocity from drift bottles without supporting current measurements. By enlarging or contracting the arc of the assumed drift tract, the apparent velocity of bottles circling the gulf may be made to vary widely. Lacking current metre data for the period of the present investigations, it has been considered advisable to use the observed interval of time required for the passage of drift bottles be-

tween various points, rather than the estimated velocity, for application to zooplankton dispersal in the gulf of Maine. However, since the present data on the rate of nontidal circulation in the bay of Fundy accords with previous records, it may be assumed that velocities in the gulf were equally comparable in May and June in 1932, and probably averaged about three to four miles per day.

The velocity of the drift about the gulf is greatest in the spring, and thereafter varies somewhat in different localities both in rate and direction according

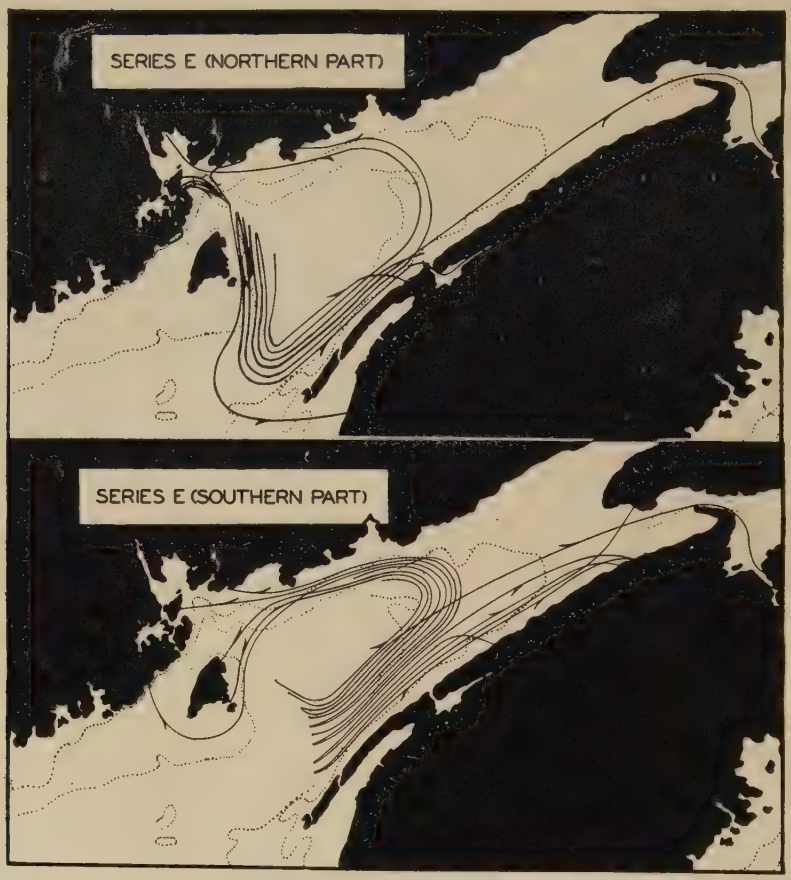

FIGURE 13 (part)

to the location of the centre of the circulatory movement. In regard to seasonal variations Bigelow (1927, p. 975) found ". . . the circulation centering chiefly around the Eastern Channel in March with velocities greatest as it drifts inward along the eastern side and outward along the western side of the latter. From March to April, however, the center of circulation shifts northward across the basin; the movement slackens in the southeastern part of the area, and the coastwise drift gathers strength. Shortly thereafter, when the water of the Nova

Scotian current floods into the Gulf from the east, the heavy center is shifted southwestward across the Gulf."

In the late summer (August to October, 1922 and 1923) with the vortex of the gulf of Maine eddy located some 40 to 60 miles south of Mount Desert, Bigelow (1927, p. 904-6) concluded that due to the circuitous route, bottles liberated off Mount Desert probably covered about as long a distance to Nova Scotia as those from off cape Elizabeth, and that the former drifted westward between Penobscot

FIGURE 13 (con.). Assumed drifts of bottles recovered from series E-G, released in the bay of Fundy, May 18-23, 1932.

bay and cape Elizabeth before veering offshore. This was suggested by the time interval of bottles reaching Nova Scotia, the average for the cape Elizabeth series being 75 days and for the Mount Desert series 70 days.

In May and June, 1932 (fig. 14B), the vortex was located farther east than in August, 1923. Drift bottles from Mount Desert and even farther east entered the bay of Fundy and grounded on the New Brunswick shore in 49 to 53 days, whereas bottles from off Casco bay yielded few returns, those reaching the same

area requiring 102 days. With the centre of the eddy in the extreme northeastern part of the basin, the drift probably veered offshore in the vicinity of Mount Desert. With an average velocity of four miles a day, bottles of series C and D (western part) placed between Mount Desert and Moose Peak could hardly have drifted much farther west than Blue Hill bay. To reach the New Brunswick coast in 49 to 53 days and at the same time travel westward to points between Penobscot bay and cape Elizabeth before veering offshore would have required an average velocity of six to seven miles, a rate obviously excessive. The higher percentage of returns from bottles placed east of Casco bay (25 per cent east of Mount Desert, 17 to 19 per cent Mount Desert to Penobscot bay, 7.5 per cent Casco bay) offers further evidence that these took a more direct and inside route to Nova Scotia.

The average and minimum intervals of drift between various points in the gulf of Maine and bay of Fundy in 1932 are shown in the following table.

Considering first the western area, eggs and larvae produced in the region

TABLE I. Distribution and interval of drift of bottles set

Area					Gulf of Maine			
					East of Mt. Desert			West
		Set out	Returned			Interval		
			No.	%	%	Min.	Av.	%
A	Off Casco bay	May 31	3	7.5	33.3	102	102	-
B	Off Penobscot bay	May 30	11	19.3	-	-	-	27
C	Mt. Desert to Great Duck island	May 26-7	4	25	-	-	-	100
D	Off Mt. Desert island	May 27	7	17.5	-	-	-	-
D	Off Moose Peak to Frenchmans bay	May 24	15	25	13	7	67.5	20
D	Off Grand Manan bank to Moose Peak	May 24	11	25	27	83	115	10
E	So. Wolves Bank (northern part)	May 23	20	31	15	8	20	-
E	So. Wolves Bank (southern part)	May 23	7	35	-	-	-	-
F	Grand Manan Channel	May 18	8	33	25	26	115	12.5
G	East and south of Grand Manan	May 18	8	25	12.5	166	166	-
H	East and south of Grand Manan	June 26	7	25	-	-	-	14
I	Off Mt. Desert	June 28	4	18.2	-	-	-	-

*Average of 5 of 7 bottles = 49 days (l = 140; l = 203)
†Average of 3 of 5 bottles = 59 days (l = 129; l= 166)
‡Average of 3 of 4 bottles = 109 days (l = 176)

between Mount Desert and Penobscot bay in May and June might have reached the bay of Fundy in a minimum interval of 31 days and an average of from 50 to 60 days. This estimate applies only to objects in the surface drift. The rate of subsurface movement, although not yet determined, is slower. Farther west, allowing 25 to 30 days (p. 209) for the circuit of the bay of Fundy, the two bottles from off Casco bay recovered in the vicinity of the Quoddy region after 102 days, probably reached the Nova Scotian coast in from 70 to 75 days, a figure approximating some of Bigelow's records for June, 1922.

The eastern region (east of Petit Manan), with relatively homogeneous water resulting from violent mechanical (tidal) mixing, forms a "dead area" in which the dominant set may, at least at times, be retarded and bottles retained locally for some time. This is indicated by the average period of drift (115 days) for all bottles set out between Frenchmans bay and Grand Manan bank (series D and H). Those liberated between Mount Desert and Moose Peak reached the

Nova Scotian coast in a minimum of 50 days and an average of 94 days. Between Moose Peak and Grand Manan bank the minimum interval of passage to Nova Scotia was 37 days, and the average 70 days.

Thus zooplankton produced west of Mount Desert, if it remained in the surface layer, might be expected to enter the bay of Fundy at an age of from one to two months, covering the greater distance as quickly, if not quicker, than forms produced in the coastal region east of Frenchmans bay. In the latter area a significant portion of such locally produced animals as survive in turbulent waters would have ample time to become well advanced in development within the immediate region.

Those branches of the coastwise drift which continue west past cape Cod and around the eastern end of Georges bank do not enter into the present problem involving the origin of the zooplankton population of the bay of Fundy. They do, however, transport out of the gulf considerable quantities of zooplankton pro-

out in the bay of Fundy and gulf of Maine in May and June, 1932

	Nova Scotia							New Brunswick					
of Mt. Desert	East to Digby			Minas Basin				coast			Grand Manan		
Interval			Interval			Interval			Interval			Interval	
Min.	Av.	%	Min.	Av.	%	Min.	Av.	%	Min.	Av.	%	Min.	Av.
-	-	-	-	-	33.3	115	115	33.3	102	102	-	-	-
139	172	64	31	84*	-	-	-	-	-	-	9	118	118
6	21.4	-	-	-	-	-	-	-	-	-	-	-	-
-	-	58	32	57.5	14	107	107	14	114	114	14	28	28
159	19.7	34	50	94#	13	110	114	7	132	132	13	114	129
235	235	27	37	69.7	36	109	126"	-	-	-	-	-	-
-	-	20	15	88	10	111	113	40	8	54	15	3	47
-	-	14	36	36	57	82	106	29	16	23	-	-	-
181	181	-	-	-	-	-	-	50	12	36	12.5	111	111
-	-	25	79	106	25	113	114	25	30	66	12.5	51	51
139	139	14	72	72	29	78	102	14	49	49	29	73	80.5
-	-	25	199	199	25	108	108	25	53	53	25	199	225

duced along the coast of Maine. Schroeder (1930, p. 87) has estimated, on the basis of previous drift bottle and current measurements, that during the winter and spring coastal drift velocities from eastern Maine to cape Ann range from five to eight miles per day, and across Massachusetts bay from two to five miles. Velocities of this order of magnitude would permit pelagic eggs and larvae of even temporary members of the plankton community, such as the cod, to travel from eastern Maine to beyond cape Cod before seeking the bottom, a condition which has led Schroeder (1930, p. 90) to conclude that the region east of cape Elizabeth to the bay of Fundy constitutes one of the most probable sources of cod fry found on the bottom on Nantucket shoals. Unfortunately it is not possible to estimate on the basis of available data what proportion of the zooplankton population is removed from the gulf in this manner.

TABLE II. Drift bottle records; May and June, 1932

Series A: May 31, 1932; four bottles at intervals of 5 miles on a line running 141° for 45 miles from a point 5 miles off Sequin island: Nos. 366-405.

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
371	43	09	54	69	11	20	L'Etang river, Charlotte Co., N.B.	Sept. 9	102
373	43	09	54	69	11	20	Eastern side of Moose cove, Me.	Sept. 9	102
379	43	16	42	69	19	00	3 miles west of Harbourville, Kings Co., N.S.	Sept. 22	115

Series B: May 30, 1932; four bottles at intervals of 2 miles on a line running 137° for 30 miles from a point 5 miles off Matinicus rock. Nos. 309-55.

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
309	34	42	19	68	47	00	3 miles east of Digby gut, Bogey brook, Digby Co., N.S.	July 19	51
314	34	40	56	68	45	15	4 miles W.N.W. Boars Head light, Tiverton, N.S.	July 8	40
320	34	39	33	68	43	30	Small point (near Bath), Me.	Oct. 9	139
325	34	38	10	68	41	45	2 miles west of Centreville, N.S.	June 29	31
338	43	32	38	68	33	45	Near coast guard station south of Strait-mouth island (near Rockport), Mass.	Dec. 4	189
342	43	31	15	68	32	00	5 miles west of Pt. Prim light, N.S.	June 30	32
344	43	31	15	68	32	00	¼ mile from Hampton wharf, Hampton, N.S.	Dec. 18	203
348	43	29	52	68	30	15	Abreast Old Harbor coast guard station, Chatham, Mass.	Dec. 3	188
349	43	29	52	68	30	15	Cow passage, White Head, Grand Manan, N.B.	Sept. 24	118
352	43	28	29	68	28	30	Youngs cove, Annapolis Co., N.S.	Aug. 28	91
355	43	27	06	68	26	45	Cape cove (near Mavillette) Digby Co., N.S.	Oct. 16	140

Series C: May 26-27, 1932; four bottles at intervals of 2 miles on a line from Bakers island to Great Duck island and then 137° for 20 miles. Nos. 253-256 (May 26); 257-308 (May 27).

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
256	44	15	15	68	10	15	South of Great Hen island (near Swan island), Me.	May 31	6
257	44	11	45	68	10	15	Cundys harbor, Casco bay, Me.	July 24	58
260	44	11	45	68	10	15	High Head point, Casco bay, Me.	June 23	28
267	44	05	00	68	10	15	Big Green island (near Matinicus), Me.	June 10	15
271	44	03	36	68	08	21	Chance harbour, St. John Co., N.B.	Sept. 17	114
273	44	02	12	68	06	32	1 mile east of Burns cove, Digby Co., N.S.	Aug. 29	95
290	43	56	36	67	59	16	Off Centreville, Digby Co., N.S.	July 13	47
293	43	55	12	67	57	27	Life saving station, Bay View, Digby Co., N.S.	July 21	56

TABLE II, Series C.—*Continued*

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
294	43	55	12	67	57	27	2 miles off Point Prim light, Digby Co.,N.S.		
296	43	55	12	67	57	27	7 miles south of Gannet Rock light, Grand Manan, N.B.	June 23	28
308	43	51	00	67	52	00	3 miles west of Harbourville, N.S.	Sept. 11	107

Series D: May 24, 1932; four bottles at intervals of 2 miles on a line running 124° for 10 miles from a point 5 miles off Moose Peak, and then 84° for 20 miles. Nos. 149 to 252.

No.	Released						Recovered	Date 1932-3	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
149	44	21	30	66	47	00	Near Harbourville, Kings Co., N.S.	Sept. 10	110
155	44	21	18	66	49	46	Johnson cove, Rogue bluffs, Me.	Oct. 16	146
160	44	21	06	66	52	32	10 miles W.N.W. of Boars head, Tiverton, N.S.	July 28	75
165	44	20	42	66	58	04	East of Mount Desert rock	Aug. 15	83
173	44	20	18	67	03	36	Diligent river, N.S.	Nov. 15	176
174	44	20	18	67	03	36	Moody beach, Me.	Jan. 13	235
178	44	20	06	67	06	22	½ mile N.E. of Little River light, Cutler,Me.	Sept. 16	116
180	44	20	06	67	06	22	2 miles west of Centreville, N.S.	June 29	37
190	44	19	30	67	14	40	3 miles west of Harbourville, N.S.	Sept. 10	109
194	44	20	50	67	17	00	Twiners brook, near Harbourville, N.S.	Sept. 10	109
201	44	22	54	67	22	00	Burns cove, Digby Co., N.S.	Aug. 29	97
211	44	24	58	67	27	00	Ross island, Grand Manan, N.B.	Oct. 15	145
212	44	24	58	67	27	00	Grosses Coques, Digby Co., N.S.	Nov. 5	166
213	44	25	00	67	29	06	Nauset harbor, cape Cod, Mass.	Oct. 29	159
215	44	25	00	67	29	06	7 miles S.W. of Boars head, N.S.	July 14	51
218	44	23	00	67	31	12	Cheneys island, Grand Manan, N.B.	Sept. 14	114
223	44	22	00	67	33	18	Victoria harbour, Kings Co., N.S.	Sept. 18	118
224	44	22	00	67	33	18	Comeauville wharf, Digby Co., N.S.	Sept. 29	129
233	44	19	00	67	39	36	Gilbert cove, Digby Co., N.S.	Aug. 7	75
237	44	18	00	67	41	42	White cove, St. Bernard, N.S.	July 13	50
240	44	18	00	67	41	42	Near Victoria wharf, N.S.	Sept. 10	110
243	44	18	15	67	52	00	½ mile N.W. of Great Wass island coast guard station, Me.	Sept. 28	128
245	44	18	30	67	59	00	East side Huppers island, Port Clyde, Me.	Nov. 2	163
248	44	18	30	67	59	00	Big Sturgeon cove (near L'Etang), N.B.	Oct. 2	132
249	44	18	45	68	05	00	Race Pt. light, Provincetown, cape Cod, Mass.	Jan. 28	250
251	44	18	45	68	05	00	2 miles N.E. of Egg rock, Frenchmans bay, Me.	May 30	7

TABLE II.—*Continued*

Series E: May 23, 1932; four bottles at intervals of two miles on a line running 142° for 30 miles from a point 3 miles off White Horse island, and then 167° for 10 miles. Nos. 65 to 148.

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
65	44	57	09	66	47	39	Broad cove, Esteys head, Eastport, Me.	May 30	8
67	44	57	09	66	47	39	Adams island, N.B.	June 9	18
69	44	55	51	66	46	12	Baileys Mistake harbor (near Jims head) Me.	May 30	8
73	44	55	33	66	44	45	2 miles from W. Quoddy life saving station, Lubec, Me.	June 7	16
75	44	55	33	66	44	45	Near Meteghan river wharf, N.S.	Nov. 5	167
76	44	55	33	66	44	45	Seeleys basin, N.B.	May 31	9
78	44	53	15	66	43	18	Tower Granville, Annapolis Co., N.S.	Oct. 17	148
80	44	53	15	66	43	18	Campbells cove, East Dipper harbour, N.B.	Oct. 26	157
84	44	51	57	66	41	51	1 mile north of Old Proprietor ledge, Grand Manan, N.B.	May 25	3
85	44	50	39	66	40	24	3½ miles W. of Harbourville, N.S.	Sept. 11	116
89	44	49	21	66	38	57	6 miles off Pt. Prim light, N.S.	June 6	15
90	44	49	21	66	38	57	Bocabec bay, Charlotte Co., N.B.	Oct. 28	159
101	44	45	27	66	34	36	Gullivers cove, Digby Co., N.S.	June 14	23
106	44	44	09	66	33	09	12 miles S.E. of Musquash light, N.B.	June 8	17
111	44	42	51	66	31	42	3½ miles west of Harbourville, N.S.	Sept. 11	111
117	44	40	15	66	28	48	Whale cove, North head, Grand Manan, N.B.	June 19	28
118	44	40	15	66	28	48	Cheneys island, Grand Manan, N.B.	Sept. 11	111
123	44	38	57	66	27	21	7 miles off Musquash light, N.B.	June 7	16
125	44	37	39	66	25	54	Eastern end Bains island (near Deer island) N.B.	July 6	45
126	44	37	39	66	25	54	¼ mile off Moose River point, Me.	June 27	36
129	44	35	03	66	24	27	N. Moose island (near Beaver harbour), N.B.	June 20	29
133	44	33	45	66	23	00	Near Victoria harbour, Kings Co., N.S.	Sept. 18	119
136	44	33	45	66	23	00	11 miles S.E. Lorneville breakwater, N.B.	June 7	16
139	44	28	00	66	21	10	3 miles E. of Parkers cove wharf, Annapolis Co., N.S.	June 27	36
143	44	28	00	66	21	10	¾ mile east of Morden breakwater, N.S.	Sept. 10	110
145	44	23	30	66	20	00	Victoria harbour, N.S.	Sept. 11	111
147	44	23	30	66	20	00	In Advocate harbour, N.S.	Aug. 13	82

Series F: May 18, 1932; four bottles at intervals of 1 mile on a line from West Quoddy Head to Whale Cove. Nos. 41 to 46.

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
45	44	48	15	66	54	39	Spruce island, Charlotte Co., N.B.	May 30	13
46	44	48	15	66	54	39	Between Chance and Dipper harbours, Charlotte Co., N.B.	Aug. 28	103
51	44	47	48	66	53	33	South end of Low Duck island, Grand Manan, N.B.	Sept. 6	111
54	44	47	21	66	52	27	½ mile north of Little River light, Me.	June 12	26
55	44	47	21	66	52	27	Petit Manan island, Me.	Nov. 16	183
62	44	46	27	66	50	15	Wooden Ball island (off Rockland), Me.	Nov. 14	181
63	44	46	27	66	50	15	Herring cove, Campobello island, N.B.	May 29	12
64	44	46	27	66	50	15	Wilsons Beach, Campobello island, N.B.	June 2	16

TABLE II.—*Continued*

Series G: May 18, 1932; two short sections along the south-east side of Grand Manan; (1) four bottles (nos. 25-32) at 11½ and 16 miles off Swallow Tail light (93°); (2) four bottles (nos. 13 to 24) at 3, 5, and 8½ miles off the northern end of White Horse island (95°). May 19, 1932; four bottles (nos. 1 to 12) at three points off Old Proprietor whistle; 4 miles (278°), 3 miles (217°), and 4 miles (154°).

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
1	44	32	43	66	43	45	Pea Pt. light, N.B.	Aug. 28	102
2	44	32	43	66	43	45	Bear cove, Digby Co., N.S.	Sept. 26	132
4	44	32	43	66	43	45	Morses point (near Popham beach), Me.	Oct. 30	166
13	44	38	18	66	33	00	Long island, N.B.	July 8	51
14	44	38	18	66	33	00	½ mile E. of Morden breakwater, N.S.	Sept. 10	115
19	44	38	20	66	36	25	2 miles N.W. from Whipple point, Briar island, N.S.	Aug. 5	79
26	44	45	25	66	32	15	West side Morden breakwater, N.S.	Sept. 9	113
30	44	45	20	66	28	00	10 miles S.S.W. of Negro head, N.B.	June 17	30

Series H: June 26, 1932, four bottles at intervals of 5 miles on a line running 124° for 15 miles from a point 5 miles off Moose Peak, and then 76° for 15 miles. Nos. 406 to 432.

No.	Released						Recovered	Date 1932	Interval (days)
	Latitude			Longitude					
	°	′	′	°	′	″			
413	44	20	30	67	00	44	7 miles east of Digby, Delaps cove, N.S.	Sept. 5	72
414	44	20	30	67	00	44	Bennetts bay, Kings Co., N.S.	Oct. 31	128
419	44	20	00	67	07	36	2 miles N.E. of North head, Grand Manan, N.B.	Sept. 6	73
423	44	19	30	67	14	28	Whale cove, North head, Grand Manan, N.B.	Sept. 21	88
425	44	22	15	67	20	43	Adams island, N B.	Aug. 13	49
426	44	22	15	67	20	43	3 miles west of Harbourville, N.S.	Sept. 11	78
427	44	22	15	67	20	43	Point of Pines, Revere, Mass.	Nov. 11	139

Series I: June 28, 1932; four bottles at intervals of four miles on a line running 137° for 20 miles from a point 5 miles off Great Duck island, Nos. 433 to 454.

No.	Released						Recovered	Date 1932-3	Interval (days)
	Latitude			Longitude					
	°	′	″	°	′	″			
434	44	04	30	68	11	00	Seeleys cove, Charlotte Co., N.B.	Aug. 19	53
437	44	01	48	68	07	14	Advocate beach near light, N.S.	Oct. 13	108
438	44	01	48	68	07	14	Gullivers cove, Rossway, Digby Co., N.S.	Sept. 26	91
447	43	56	24	67	59	42	White Head island, Grand Manan, N.B.	Feb. 2	251
450	43	52	42	67	55	56	Meteghan Centre, Digby Co., N.S.	Jan. 12	199

OFF SHORE WATERS

Quantitative Zooplankton Distribution

In considering zooplankton volumes one must distinguish between abundance (richness) of the adult population and productivity. The difference results from the time interval involved in the development of planktonic animals, which may range from a few weeks to several months. With the active circulation in the gulf of Maine it is probable that very few, if any, of the offshore species reach maturity very near their point of origin. A locality might thus be relatively unproductive and yet at times harbour an abundant population consisting largely of immigrants from other breeding areas so situated as to serve as sources of supply. Such a condition exists in Frenchmans bay. The quantitative distribution of the adult stock, therefore, can be considered to serve as a measure of the result of production on various areas but does not in itself necessarily indicate the source

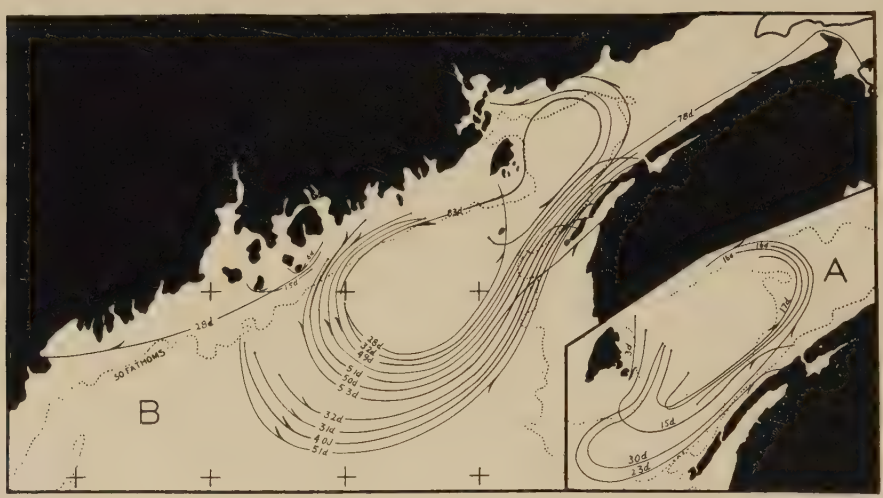

Figure 14. Maximum interval of drift of certain bottles released in (A) the bay of Fundy on May 19-23, and (B) the gulf of Maine in May and June, 1932.

of origin. To gauge the productivity of an area one must consider the amount of actual successful propagation taking place there. This, however, involves different methods of analysis, which have been treated separately elsewhere (Fish 1936a, 1936 b and c).

The quantitative distribution and seasonal changes in the abundance of zooplankton in the gulf of Maine as described in detail by Bigelow (1926, p. 78) agree very well with the present findings. The purpose here will be to consider the bay of Fundy in relation to the gulf and to compare the records for 1931-32 in the latter area with those previously obtained. Unfortunately, due to different methods used, it is not possible to compare the actual volumes obtained in the present investigation with those of Bigelow. The relative differences in quantitative distribution are comparable however.

In analyzing the collections prior to April, 1932, when only horizontal towing was carried on (p. 194), the volumes obtained by 20 minute hauls with a closing metre net at the surface and lower levels have been combined and the results adjusted for a towing interval of 40 minutes. This is not a very satisfactory method as it does not allow for possible concentrations of animals in layers not included in the hauls. It does serve to indicate wide differences in abundance, however, and has been used in this manner to supplement the more accurate results which added facilities made possible during the second season. Beginning with cruise 26 on April 15, 1932, volumes were based on oblique tows and represent a metre net haul of 40 minutes duration through the total column of water. For vertical differences in distribution each haul was made in two parts, the first from the bottom to 50 metres and the second from 50 metres to the surface.

APRIL TO SEPTEMBER

Bigelow (1926, pp. 82-83) found that in 1920 the animal plankton of the gulf as a whole was at its lowest ebb in late February and during the first half of March. Later in March propagation began in Massachusetts bay and gradually spread seaward and to the east. General augmentation he found evident in April across the southern half of the gulf from the mouth of Massachusetts bay to the coastal bank off cape Sable, and including the eastern part of Georges bank. North of a line from cape Cod to cape Sable the records for 1920 indicated no increase, and in the northeastern part of the basin an unmistakable decrease in the amount of zooplankton took place from March to April coincident with the local flowering of diatoms.

It was at this season (April 15 to May 2) that investigations in the gulf of Maine began in 1932. Vernal propagation was taking place over a considerable portion of the gulf (Fish 1936a, fig. 5; 1936b, fig. 5) but its influence upon the adult population was as yet restricted to a very limited area. Elsewhere volumes were for the most part at the winter minimum. The mean volume for the total region included in the investigations was at this time 86 cc., that of the gulf of Maine 110 cc. and the bay of Fundy 62 cc. The latter area extended as far east as cape Spencer. Beyond this point in the headwaters of the bay eight hauls taken by the Nova IV (sta. 170-177) in April yielded a mean volume of only 29 cc.

The quantitative distribution of animal plankton in April is shown in figure 15. Vernal augmentation was particularly suggested in the most western line of stations in the gulf where the greatest volume, 870 cc., was obtained at station 26. Here 715 cc. of the total amount occurred in the upper 50 metres with juvenile *Calanus finmarchicus* comprising 42 per cent of the population. Young of this species also formed 37 per cent of the lower haul from 125 to 50 metres. (Species percentages indicate relative numerical values and not relative volumes.) It is in the upper 50 metres (fig. 15), where juvenile stages occur in greatest abundance, that the influence of recent propagation would be expected to be most readily detectable. Due, however, to the small parent stock remaining in both the gulf

and bay of Fundy, hauls through the total column of water indicated these conditions equally well.

It would appear that in 1932 the reproduction season began somewhat earlier than in 1920, and the line marking the limit of general augmentation of the adult population had by the end of April moved eastward to the vicinity of Casco bay.

FIGURE 15. Quantitative distribution of zooplankton in April, 1932. Volumes measured by the displacement method.

North of a line from Casco bay to cape Sable the volumes were uniformly low and ranged from 6 cc. to 90 cc. with the exception of one station (37) on the Nova Scotian side of the bay of Fundy where a local swarm of large adult *Sagitta elegans* (probably from the outer part of the gulf of Maine, Bigelow 1926, p. 41) comprising 49 per cent of the haul yielded a volume of 155 cc. The most barren

area, with volumes ranging from 6 cc. to 19 cc., extended along the coast from the vicinity of cape Spencer to Penobscot bay. Throughout the summer this region contained the smallest adult population and showed the least influence of propagation as indicated by the presence of eggs, larvae and juvenile adults. The western boundary of the barren area varied during the season from Penobscot bay to Petit Manan, but more commonly it was found to terminate in the vicinity of Mount Desert. Bigelow (1926, p. 83) observed that the coastal area east of Penobscot bay was similarly barren in April, 1915.

As the dominant members of the zooplankton population, including *Calanus finmarchicus, Pseudocalanus minutus* and all four local species of *Thysanoessa,* begin reproducing in March and April and are soon followed by another important form, *Meganyctiphanes norvegica,* it was to be expected that metre net collections would show rapid restocking by late juveniles in May. The mean volume for the total region during the period May 19-31, 1932, was found to be 385 cc., an increase of 348 per cent over the previous month. This increase affected both the gulf of Maine and the bay of Fundy where the mean volumes amounted to 497 cc. (351 per cent increase) and 274 cc. (342 per cent increase) respectively. The richest zone continued to be centred in the western part of the gulf but the boundary had advanced northward to include the outer stations of sections to the east, and stations extending into the bay of Fundy along the Nova Scotia side (fig. 16). Station 37 again yielded a large haul, in fact the greatest volume taken on the cruise, but vernal augmentation now accounted for the size of the catch. In the upper haul juvenile *C. finmarchicus* formed 69 per cent and in the lower 53 per cent of the population. *Sagitta elegans* still formed 20 per cent of the lower haul but had declined considerably from the previous month. Comparatively rich hauls were regularly taken in the central deep portion of the bay and will be discussed later (p. 231).

The New Brunswick-eastern Maine coastal area still yielded the smallest volumes, the Quoddy region having increased only from 11 cc. to 20 cc. during the month, and in the vicinity of Saint John the quantities actually declined at sta. 11 and 12, the latter from 90 cc. to 31 cc. A similar condition was found in May, 1915, by Bigelow (1926, p. 83) who reported an increase by the end of the month throughout the gulf outside of the 50 metre contour with the exception of the coastal zone eastward of Penobscot bay. The relative distribution of high plankton volumes figured by Bigelow (1917, p. 313) was also markedly similar to that of 1932. The western boundary of the very barren area in 1932, due to the more advanced season, had by the end of May contracted eastward to the vicinity of Petit Manan. The peak of the season in the gulf was reached in May and thereafter a gradual decline took place throughout the following months. This also accords closely with the observations of Bigelow, who found the greatest mass of animal plankton during the last week in May and the first of June. By the end of June in 1932 the volume for the total region had declined to 299 cc., a decrease of 22 per cent. The decrease was most noticeable in the gulf (fig. 16) where the mean volume declined 38 per cent, *i.e.* to 308 cc.

In the bay of Fundy where the seasonal response was slower, the mean volume continued to increase slowly (6 per cent to 290 cc.) after the decline had set in in the gulf. The peak here was reached in June with the largest volumes occurring along the Nova Scotian side of the bay.

Although juveniles were more generally distributed throughout the total area

FIGURE 16 (part)

at this time, the relative quantitative distribution was strikingly similar to that of the previous two months. Sta. 37 again yielded the greatest quantity (*C. finmarchicus* and *P. minutus* forming 91 per cent in the upper haul and 85 per cent in the lower), and the New Brunswick-eastern Maine coastal area the smallest. The influence of restocking was everywhere evident in the latter area except in the vicinity of Saint John where the volume at sta. 12 was still below that of April.

As the June cruise terminated on July 1 an interval of five weeks was allowed before beginning the next on August 8. By this time a further reduction of 29 per cent to 213 cc., had taken place in the total area. The most rapid decline was now found in the bay of Fundy (42 per cent) and was remarkably similar to that of the gulf during the previous month (38 per cent). The rate of reduction

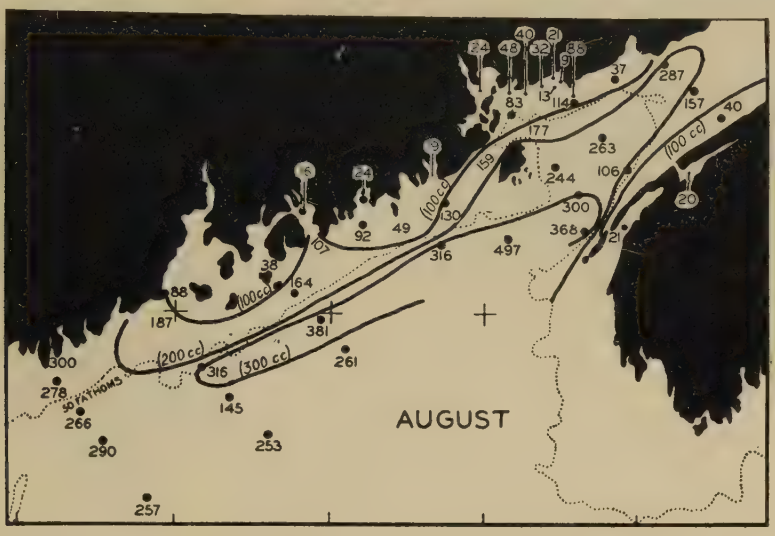

FIGURE 16 (con.). Quantitative distribution of zooplankton in May, June and August, 1932. Total volumes (displacement).

of the stock in the gulf appeared to have become slower, the mean volume of 257 cc. being but 17 per cent lower than that of late June.

The quantitative distribution of animal plankton now indicated a changing centre of abundance. During April, May and June the southwestern portion of the gulf had first increased in volume and later expanded to the east and into the bay of Fundy along the Nova Scotian shore. By August the volumes in the southwestern area had declined to amounts approximating those of the central portion of the bay of Fundy. The relatively barren New Brunswick-eastern Maine coastal area still persisted, but the richest hauls indicated by the 300 cc. curve (fig. 16) were now centred in a belt whose inner margin paralled the 50-fathom contour and extended from off Penobscot bay diagonally across the entrance of the bay of Fundy to the vicinity of the Boar's Head, Nova Scotia. A similarly rich belt, but broader and extending to Massachusetts bay, was found by Bigelow (1917, p. 308; 1926, p. 84), in 1913, 1914 and 1915, and is considered to be a typical summer condition, after the decline of the cold Nova Scotian drift described on pp. 195 and 312.

A continued decline in the adult stock of 27 per cent (155 cc.) took place over the total region in September. At this time the mean volume in the bay of Fundy had fallen to 119 cc. (–30 per cent) and in the gulf of Maine 198 cc. (–23 per cent). The stations in the latter area were too widely separated on the

September cruise to permit the drawing of detailed contours, but the conditions in the bay of Fundy indicated a quantitative distribution similar to that of August.

It was not possible to include on the routine cruises two areas reported by Bigelow (1917, p. 308) to be rich in summer, over the northeastern portion of Georges bank and from cape Sable out to Browns bank. The range was extended on a special cruise in September, 1932, and one station taken in each of these areas. Sta. A 1410, west of cape Sable, yielded a relatively high volume of 387

FIGURE 17. Quantitative distribution of zooplankton in September, 1932. Total volumes (displacement).

cc., suggesting that conditions in 1932 were here similar to those in 1914. At sta. A 1414 on the northeastern portion of Georges bank a volume of 100 cc. was obtained. This is relatively small contrasted with the other area and also with two stations taken farther west over the central portion of the bank. There at sta. A 1415 the volume was 440 cc. and at sta. A 1416, 248 cc. (*Centropages typicus* population).

Repeated high volumes taken at sta. 35, 36, and 37 in the bay of Fundy sug-

gest that the central area may form a vortex where zooplankton tends to temporarily accumulate due to the nature of the circulation about the bay. Again it is probable that the volumes over much of the bay are larger than might be expected because this area forms a sort of funnel, small in size when contrasted with the gulf. Animals entering the bay in the surface drift as regularly and constantly as drift bottles indicate would tend to be more concentrated there. This is merely mentioned as a point to bear in mind in comparing volumes in the two areas.

Sufficient data are not available to permit a satisfactory comparison of the quantities of animal plankton in 1931 and 1932. It was possible to take but one cruise in the bay of Fundy and gulf of Maine during the first season, and as the stations in the latter area were located nearer the coast than in the following year

FIGURE 18. Variation in the mean volume (displacement) of zooplankton in the gulf of Maine and bay of Fundy during the principal period of augmentation in 1932.

they are not considered comparable. The mean of three gulf stations taken in both years (15, 17, 25-25A) amounted to 519 cc. in August 1931, and 945 cc. in August 1932. This small number of stations scattered over such a wide area is not sufficient to overcome differences due to local irregularities in distribution, and these figures are of significance only in that they indicate that the plankton in the gulf was far greater than in the bay during the two summer seasons. In the bay of Fundy the stations in September covered the same area and, although more observations were made in 1932, the mean volume indicates approximately the same amount of zooplankton present at that time in both years.

Year	Date	Mean volume (settling)
1931	September 1- 5	350 cc.
1932	September 14-26	335 cc.

TABLE III. Volume of zooplankton. Oblique metre net hauls adjusted to 40 minutes. Measurements by displacement method

Cruise	Date 1932	Total area			Gulf of Maine			Bay of Fundy		
		Mean volume cc.	Factor	% change	Mean volume cc.	Factor	% change	Mean volume cc.	Factor	% change
Bottom to surface										
26	Apr. 15-May 2	86	1		110	1		62	1	
27	May 19-May 31	385	4.5	348	497	4.5	351	274	4.4	342
28	June 20-July 1	299	3.5	−22	308	2.8	−38	290	4.7	6
30	Aug. 8-Aug. 21	213	2.5	−29	257	2.3	−17	169	2.7	−42
32	Sept. 14-Sept. 26	155	1.8	−27	198	1.8	−23	119	1.9	−30
Fifty metres to surface										
26	Apr. 15-May 2	102	1		158	1		46	1	
27	May 19-May 31	544	5.3	433	718	4.5	354	368	8	722
28	June 20-July 1	300	2.9	−45	300	1.9	−58	302	6.5	−18
30	Aug. 8-Aug. 21	222	2.1	−26	284	1.8	−5	160	3.5	−47
32	Sept. 14-Sept. 26							152	3.3	−5

Factor indicates the ratio to April volume.
Percentage change refers to preceding month.

Reviewing conditions throughout the summer season in 1932, with the beginning of vernal augmentation in March and April the zooplankton stock rose

rapidly from a winter minimum as low as 11 cc. in New Brunswick waters. As shown in figure 17, the mean volume over the total area increased 348 per cent from April to May. Reaching a peak in the gulf in late May and a month later in the bay, a summer decline followed, in spite of subsequent propagation, until by the end of September the stock had decreased 60 per cent in the gulf and 59 per cent in the bay of Fundy. At all times the quantity of zooplankton in the gulf was larger than in the bay, although the relative seasonal fluctuations in volume (fig. 18) and general nature of the community were very much the same.

Observations in the gulf terminated before the autumnal augmentation which precedes the long winter decline to the yearly minimum, but these changes are indicated in the following records obtained in the bay of Fundy during the winter of 1931-32.

FIGURE 19. Quantitative distribution of zooplankton in August-September, 1931. Total volumes (settling).

WINTER CONDITIONS

Following the termination of the summer investigations in September, 1931, routine observations were continued through the winter at three stations in the bay of Fundy. Figure 20 gives the mean volume for September, November and December at two stations on a line across the entrance to the bay just east of Grand Manan. Sta. 8A was selected to indicate the population entering from the gulf of Maine, and sta. 6 that passing out along the east side of Grand Manan after circling the bay.

The decline in volume continued during October and early November at both stations, although the character of the population throughout the bay of Fundy, particularly in the upper level, was changing due to late fall augmentation of *Centropages typicus*. Copepodites of this species were taken in increasing abundance in August and by September formed an appreciable part of the population (pp. 306-307). Their numbers, however, were insufficient to conteract the de-

cline of other species until late November when the volume (settling) at sta. 8A rose rapidly from 279 cc. to 1160 cc. Judging from summer conditions the changes at this station would more closely approximate those in the gulf than in the bay of Fundy proper, although the response would be expected to be at least a month later than in the western area.

Support for this opinion is found in Bigelow's (1926, p. 87) records, "Vertical hauls in the Massachusetts Bay Region, the only part of the Gulf where our data warrant even a tentative account of the quantitative fluctuations that take place during late summer and autumn, suggest a diminution in the volume of zoo-

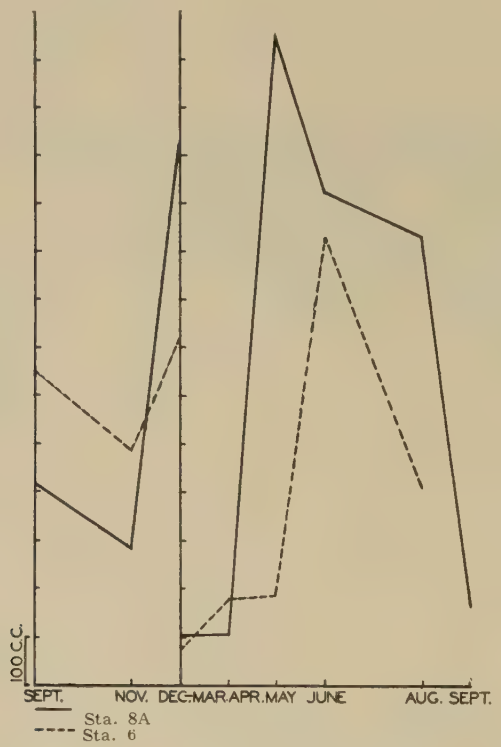

FIGURE 20. Seasonal variation in the volume of zooplankton at stations 6 and 8A in the bay of Fundy during the periods, September-December, 1931, and March-September, 1932. Average monthly volumes (settling).

plankton during the late summer followed by an autumnal increase, which was so considerable in 1915 that there was over twice as much plankton per square metre in water only 80 metres deep by the end of October as we had found at a neighbouring station in 140 metres depth two months previous."

If sta. 6 be considered characteristic of the bay of Fundy and sta. 8A as indicative of the adjacent part of the gulf of Maine, the volume within the bay was greater than the eastern gulf area from September to November but the rate of decline was approximately the same. The rapid rise in late November was most

marked at sta. 8A where an increase of 316 per cent took place. At sta. 6 the response was slower and by December amounted to only 50 per cent. Due to a fire, samples taken in January and February were destroyed and whether or not the December records represented the winter maximum in the bay could not be determined, but by March volumes had declined to 74 cc. at sta. 6 and 105 cc. at sta. 8A.

In the annual cycle of quantitative changes, the great vernal increase followed almost immediately by a sharp decline, amounting to 38 per cent in the gulf in June and 42 per cent in the bay a month later, is most striking. The period of augmentation, reflecting propagation by the dominant boreal species (p. 306), is easily understandable, but the reason for the rapid depletion may be open to question. Several possible contributing causes suggest themselves, among which are: (1) high mortality in the dominant copepod stock during maturation (p. 316) and after spawning (Bigelow 1926, p. 43); (2) dispersal from propagation centres to relatively less productive areas resulting in more even distribution of the stock; (3) animals upon reaching maturity descending to the bottom in shallow areas and to depths beyond the range of the haul in deeper areas; (4) euphausiids in later stages avoiding the nets.

1. In light of all available evidence it seems most probable that the great decline following the May-June peak is due to normal biological factors involving primarily the dominant boreal copepods. As the fluctuations in the total volume reflect to a large extent changes in the content of the most important species, *Calanus finmarchicus*, forming 35 to 40 per cent of the total zooplankton population (Fish 1936a, p. 120) in the region, the rapid downward trend in June coincides with the critical period of maturation (p. 319) combined with the subsequent mortality of adults after spawning.

Pseudocalanus minutus, forming from 5 to 10 per cent of the population (Fish 1936b, p. 213) and second in importance, also passes through a very similar cycle at approximately the same time. Biological changes in these two species alone would thus affect up to 50 per cent of the total zooplankton stock in the region.

2. Regarding dispersal, assuming that one area is unproductive and depends upon immigration from another area for its population, one would expect the response in the unproductive area to any changes in the productive area to be delayed, the time interval depending on the distance involved. Applying these considerations to the gulf of Maine and the bay of Fundy, it was found that in 1932 the May increase in the gulf was continued in the bay through June. A decline of 38 per cent in the gulf in June was followed by a drop of 42 per cent in the bay in July and early August. Similarly the seasonal reduction of 60 per cent in the gulf was reflected in the bay by a decline of 59 per cent. The decline in the former area extended over a period of four months, but once the supply was reduced a decline of like degree took place in the bay of Fundy in three months.

Were it not for other data indicating the lack of successful production in the bay of Fundy, these figures would not in themselves be conclusive because they

could be interpreted as indicating production on a smaller scale taking place later in the bay of Fundy. The close accordance of the relative fluctuations in the two areas, however, and the fact that the quantity of zooplankton in the gulf was at all times so great that it governed the mean volume for the total region throughout the season, suggests the product of that area as the dominant influencing factor.

Further evidence that the fluctuations in the bay of Fundy result from importation, and not delayed response due to differences in latitude, is indicated in figure 20 contrasting two stations within the bay itself. These stations were located only 30 miles apart (fig. 2), a distance hardly sufficient to allow for seasonal differences in local production. At sta. 8A this response followed closely

FIGURE 21. Abundance of zooplankton in the upper levels during the augmentation season in 1932. Mean volumes (displacement) based on monthly averages of all stations, adjusted to a towing period of 40 minutes.

changes in the gulf of Maine and yielded volumes at the peak of the season considerably higher than at sta. 6. Interpreted in the light of hydrographic evidence it would appear that the population at sta. 6 in June formed a part of the stock observed at sta. 8A in May. Due to dispersal throughout the bay, the volume, provided no significant local production supplemented the immigrant stock, would be expected to be smaller at sta. 6, as proved to be the case. There would thus appear to be little doubt that the stock in rich areas of the gulf is diluted by dispersal into less productive waters, but this takes place gradually and continuously throughout the summer. It is probably at best only a minor contributing factor in the sudden June depletion.

3. Animals immediately adjacent to the bottom would not be taken in an oblique haul made in the usual manner. In the present investigations the nets traversed as nearly as possible the total column of water at most stations and to depths exceeding 150 metres at the few deeper stations in the gulf. As the dominant species of *Calanus, Pseudocalanus,* and *Meganyctiphanes* in summer have been found to have their centre of abundance in the upper 100 metres (Bigelow 1926) and the present records (fig. 21) indicate that within this range the quantities in the upper 50 metres throughout the spring and summer season exceeded those below, it seems probable that the samples were representative and the decline shown in the volume curve indicated a corresponding reduction in the actual amount of animal plankton.

4. In regard to the euphausiids, the greater part of those hatched in April might not be included in the hauls after June or early July, but they would comprise largely species of *Thysanoessa* which in the region were found both as adults and young in much smaller numbers than *M. norvegica.* The latter species reached its maximum production in July and August when, even with the greatly reduced stock at the time, it did not exert any detectable influence on the declining volume curve. It would therefore appear that the absence in the net hauls of juveniles of the less abundant species would probably prove of equally minor significance, and that the first suggested cause (p. 229) is the most probable.

The downward trend of zooplankton volumes throughout the summer was rather unexpected, for all dominant spring spawning species, with the exception of *Thysanoessa,* had at least one subsequent breeding season, and that of *M. norvegica* reached its peak in July and August. Again the available parent stock in June and July was much greater than that at the beginning of the season in March. The volumes, however, show clearly that the influence of summer spawning by young adults is relatively small compared with that of the older stock in the spring. The possible cause for this will be considered later (pp. 316-317).

Composition of the Zooplankton Population

Boreal waters, contrasted with more temperate and tropical regions, are comparatively rich in individuals but notoriously sparse in the number of species comprising the zooplankton population. The contrast is further accentuated by the fact that, out of the total local population, only a relatively small number of endemic species comprise the greater part of the stock at all times. Of more than 160 species occurring in the net collections in the gulf of Maine, three or four usually account for more than 80 per cent of the total number of individuals, and frequently this percentage is much larger.

The present chapter will be devoted to a consideration of the relative composition of the total zooplankton population. In analyzing this population, particularly from the standpoint of natural economy, an attempt has been made to first determine the relative numerical importance of the various ecological groups represented. Detailed analyses of the distribution and biology of dominant in-

dividual species of the offshore stock in the region have been published elsewhere (Huntsman and Reid 1921, Bigelow 1926, Fish 1936a, 1936b and c).

Within the gulf of Maine and bay of Fundy the zooplankton stock during the course of the year is composed of the following groups: boreal endemic species, northern and southern migrants, neritic plankton species, fish eggs and larvae, larvae of benthonic invertebrates, and occasional adult benthonic invertebrates. The relative importance of the groups varies geographically and also with the seasons.

If considered only from the standpoint of natural economy, some of these groups might have been omitted entirely in the present report. However, since this forms the first attempt to determine the relative composition of the complete zooplankton stock in the region, we feel it desirable to include a comparable analysis of all groups represented even though some of the data are not applicable to the immediate problem. Only in this way can a clear conception of the population as a whole be obtained. Again anyone interested solely in the Quoddy region (p. 190) may disregard the remainder of this chapter.

TABLE IV. Composition of the zooplankton population in the bay of Fundy.

						1931
Month	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number of hauls	3	6	14	4	9	12
Endemic boreal species	91.8	89.3	93.0	98.7	99.1	99.1
Northern immigrants	.3	.7	.04	.3	.4	.3
Southern immigrants			.04		.1	T
Neritic zooplankton	5.5	9.4	2.0	.7	T	.04
Fish eggs and larvae	3.1	.2	1.5	T	T	T
Benthonic invertebrate larvae	T	T	3.2	T	T	T
Benthonic invertebrates	T	T	T			

						1917
Month	Jan.	Feb.	Apr.	May	June	July
Number of hauls	1	3	2	2	2	4
Endemic boreal species	99.0	96.6	92.3	98.1	86.3	96.5
Northern immigrants	1.0	3.3	1.9	1.1	13.8	2.9
Southern immigrants						
Neritic zooplankton			2.4	T		
Fish eggs and larvae			1.5			
Benthonic invertebrate larvae			1.9	.8		.6
Benthonic invertebrates						

RELATIVE NUMERICAL IMPORTANCE OF THE ECOLOGICAL GROUPS

Bay of Fundy. Observations were continued throughout the year only in the bay of Fundy, where of the seven groups, boreal endemic forms were found to constitute more than 80 per cent at all times, and for the greater part of the year ranged from 90 per cent to 99 per cent. Since the mean for all stations for the year October 1931 to September 1932 was 94.4 per cent, and for the period from January to December 1917 was 96.5 per cent, it would appear that the boreal group may be expected to average about 95 per cent of the total zooplankton population in the bay. Larvae of benthonic invertebrates ranked second in 1931-32 with a yearly mean of 2.9 per cent and neritic plankton species third with 1.9 per cent.

Comparing the results for the period from July to September in 1931 and 1932 in the bay, it is seen that the composition of the population was substantially the same in the two years:

	1931	1932
Endemic boreal species	91.4	92.1
Northern immigrants	.3	.4
Southern immigrants	.01	.03
Neritic species (plankton)	5.6	5.9
Fish eggs and larvae	1.6	.3
Benthonic invertebrate larvae	1.1	1.4
Benthonic invertebrates	T	T

Inner gulf. Inasmuch as the bay and adjacent portion of the inner gulf (central area) have been shown to be relatively barren as contrasted with the region west of Mount Desert, (p. 220) it is of importance to consider the composition of their respective populations, during the period from April to September, which

Relative percentages of the various ecological groups in metre net collections.

1932								
Jan.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.-Sept.
2	6	25	25	25	2	26	24	160
98.9	98.2	81.0	90.2	96.4	99.8	85.1	91.7	94.4
T	.6	.5	.1	.2	.2	T	.2	.3
	.2	T	T	.1	.1	T	T	.1
.7	.3	.2	.5	.6	.1	11.6	6.0	1.9
.2	T	.4	1.1	1.2	T	.2	.6	.3
	.4	17.6	8.1	1.2	.1	3.3	1.5	2.9
		.3	T	.2	T	T	T	.1

Sept.	Oct.	Nov.	Dec.		Jan.-Dec.
3	2	1	2		22
99.8	99.3	99.6	98.1		96.5
T	.4		2.0		2.7
		T			T
		T			.2
					.2
	.3	.4			.4

forms the principal augmentation season of open gulf species and also the time when neritic plankton species and benthonic larvae reach their peak. That this barrenness results from lack of successful propagation of open gulf species is indicated by the fact that even in the reduced population the relative percentage of this group becomes increasingly smaller to the eastward. Whereas endemic boreal species totalled 97.6 per cent in the western area, in the central area they amounted to 89.3 per cent and in the bay 88.9 per cent (table V).

Benthonic larvae, however, do not appear to be influenced to the same degree as offshore planktonic species by limiting factors and develop successfully throughout the region. Thus although the actual numbers of individuals in all groups are larger in the western gulf, the relative percentages of benthonic larvae (9.2

per cent, central area; 6.3 per cent, bay) are higher in the eastern gulf and bay.

The remaining four groups totalled 0.7 per cent in the western area, 0.8 per cent in the central area, and 1.0 per cent in the bay.

Outer gulf. Bigelow's records (1926, pp. 47-50) indicate that from late autumn until March the zooplankton is fairly uniform over a greater part of the gulf and consists largely of boreal species. However, during the period from

TABLE V. Composition of the zooplankton population from April to September,

Area	Total region						Western area		
Month	Apr.	May	June	Aug.	Sept.	Apr.-Sept.	Apr.	May	June
Cruise	26	27	28	30	32		26	27	28
Endemic boreal species	78.5	93.9	97.5	92.3	97.2	91.9	95.1	99.4	96.7
Northern migrants	.3	.2	.1	.01	.07	.13	.3	.05	.1
Southern migrants	.04	.01	.05	.1	T	.05	.02	.02	T
Neritic species	.1	.3	.6	5.3	2.0	1.7	T	.2	1.0
Fish eggs and larvae	.5	.6	1.2	.8	.2	.6	.3	.03	1.3
Benthonic invertebrate larvae	20.5	4.8	.5	1.3	.5	5.5	4.4	.3	.3
Benthonic invertebrates	.1	T	.07	T	T	.03			

April to September local production, particularly of neritic species and larval benthonic forms, would be expected to influence significantly the population of the inner gulf, and perhaps through the agency of the drift extend well out into offshore waters, particularly in the upper levels.

To determine how much more coastal conditions influence the composition of the population of the inner gulf than the offshore basin, hauls from the bottom to 50 metres at the three outermost stations (26, 29, and 31) were selected. These stations were located in the inner part of the basin where depths exceed 175 metres, and are considered generally indicative of offshore conditions. Taking the mean for the three stations on four cruises between April and August, and one station

TABLE VI. Composition of the zooplankton in different areas in May and

Year	1932			
Month	May			
Period	19-24	18-19	18	14
Area	Off Cape Ann	Western basin	Central basin	Eastern channel
Stations	N260-261	N258-259	N255-256	N245
Endemic boreal species	99.2	99.8	99.6	97.5
Northern migrants				T
Southern migrants	T	T	T	T
Neritic species	.6	.2		
Fish eggs and larvae	.2			1.5
Larvae of benthonic invertebrates	T		T	1.0
Benthonic invertebrates				

in the middle of the gulf (A1411) in September, the following values were obtained: endemic boreal species 98.8 per cent, northern immigrants 0.4 per cent, southern immigrants 0.1 per cent, other forms combined 0.7 per cent. At no time during the summer did the percentage of endemic boreal species fall below 98.2 per cent (June) and in August the percentage reached 99.7 per cent.

To these data may be added the following offshore records for May and September, 1932. It will be noted that the boreal population exceeded 90 per cent everywhere except in the bay of Fundy for a brief period in late May when *Balanus balanoides* larvae swarmed in those waters. Then the percentage declined from 90.2 per cent (May 18-23) to 72.7 per cent (May 30-June 2) but quickly rose again to 96.4 per cent by June 20 (table VI).

1932. Relative percentages of the various ecological groups in metre net collections

		Central area					Bay of Fundy				
Aug.	Sept.	Apr.	May	June	Aug.	Sept.	Apr.	May	June	Aug.	Sept.
30	32	26	27	28	30	32	26	27	28	30	32
96.9	99.8	59.2	92.1	99.5	95.1	100.0	81.0	90.2	96.4	85.1	91.7
T	T	.1	.3	.05	.04	T	.5	.1	.2	T	.2
.1	T	.1	T	.05	.3	T	T	T	.1	T	T
1.3	T	.1	.1	.1	3.1		.2	.5	.6	11.6	6.0
1.2		.9	.8	.2	1.0	T	.4	1.1	1.2	.2	.6
.1	T	39.6	6.0	.1	.5	T	17.6	8.1	1.2	3.3	1.5
T	T	T	T		T		.3	T	.2	T	T

It would thus appear that west of Mount Desert, even during the summer, endemic boreal species of the offshore population form substantially as important a part of the stock in coastal waters outside of the headlands as anywhere in the open gulf, and that in the eastern coastal region and the bay of Fundy the influence of larvae of benthonic forms and neritic species probably average less than 10 per cent.

ENDEMIC POPULATION

This term should really apply to both boreal oceanic and boreal neritic species endemic in the region, but for purposes of distinction in the present report it will be considered to apply only to the offshore species characterizing the open gulf

September. Relative percentages of the various ecological groups in metre net collections

							1931
		September					
14	30-June 2	20-23	20-24	25	23	15-16	1-5
Brown's bank	Bay of Fundy	Inner gulf	Outer gulf	Georges bank	W. coast Nova Scotia	Bay of Fundy	
N244	N273-284						
100.0	72.7	100.0	94.0	97.2	99.7	91.7	93.0
	.4	T	.6		T	.2	.04
		T	4.5	2.3	.3	T	.04
	.5	T	T			6.0	2.0
T	.2	T	T	T		.6	1.5
	26.2	T	.9	.3		1.5	3.2
	T	T		.2		T	T

community. Plankton species associated with the coast and restricted largely to relatively shallow waters will be designated as neritic.

Number of species. The boreal population includes approximately 30 species universal in the gulf and bay of Fundy. Twenty-seven of these, listed in table VII, occurred regularly at some time during the year in the metre nets, and two

additional small species, *Oithona similis* and *Microsetella norvegica,* appeared in the pump samples. A few other species, particularly copepods, of which Bigelow lists three, *Paracalanus parvus, Candacia norvegica* and *Monstrilla serricornis,* have been reported. The exact status of the two latter species is uncertain as they have as yet been found only in small numbers in Norwegian waters and the gulf of Maine. *Paracalanus* at times is widespread in the gulf (Bigelow 1926, p. 264) and the presence of a few larvae in 1932 indicates that it propagates there during the summer, but for reasons which will be discussed later (p. 250), it is considered a more temperate species in the western Atlantic, centred south of cape Cod. No specimens were taken in the net collections in either 1931 or 1932. Considering the number of observations which have been made in the gulf and bay of Fundy, it is not probable that other truly boreal species which may at times enter the region, but have escaped detection, ever prove numerically significant.

Bigelow (1926, p. 16) has previously called attention to the qualitative uniformity of the zooplankton in the open gulf throughout the year, and lists as the typical "Calanus community", *Calanus finmarchicus, Pseudocalanus minutus, Metridia lucens, Sagitta elegans, Euthemisto,* the several species of *Thysanoessa, Meganyctiphanes norvegica, Limacina retroversa, Pleurobrachia pileus,* and in deeper water *Euchaeta norvegica.* These form the most common members of the endemic group, and may be expected in collections everywhere in the open gulf at any season. (See pp. 309-310 for discussion of status of *M. lucens.* Because of the seasonal and geographical range of the adult stock it is here grouped with endemic species.)

Seasonal variation. Quantitatively, however, the composition of the population varies greatly at different times of the year and in different areas. All observed endemic forms have definite propagation periods and it is then that the relative importance of the particular species breeding at the time is usually greatest. Considered on the basis of seasonal changes, the boreal population falls into three general classes:

(1) A relatively few species such as *Centropages typicus* and *Anomalocera patersoni* all but disappear shortly after the termination of the augmentation period and occur only sparsely, if at all, within the region until the next breeding season.

(2) Other species like *Euthemisto compressa* and *Temora longicornis* are nearly always present in the gulf but, in the inner coastal region at least, appear to be of numerical significance for only a limited portion of the year.

(3) A third class, of which the copepods *Calanus, Metridia,* and *Pseudocalanus* are most important, are at all times abundant somewhere in the region, and except for a short time in autumn when *Centropages typicus* swarms in the upper levels, make up the bulk of the population over the greater part of the gulf and bay throughout the year. In the bay of Fundy in 1931-1932 these three species formed 56.3 per cent (by number) in the metre net collections, and in 1917 when *Centropages* did not swarm, they averaged 90.1 per cent.

Of the three classes it would appear that the greatest variation from year to

year occurs in the first, which most closely resembles the neritic group in being confined largely to the upper levels and almost totally absent for a part of the year. Even the most abundant member of this class, *Centropages typicus,* which swarmed in the autumn of 1931 and 1932 (p. 239) in the bay was apparently lacking at that season in 1917, appearing only in April with an average of 0.8 per cent for the month. Whether individuals of this class, like certain neritic species, pass a portion of the year in a resting stage, possibly in the form of eggs, is not known. Their restriction to the upper portion of the water mass would render them more exposed to unusual climatic conditions than the more typical boreal species with a wider vertical range. A proper allocation of *Centropages typicus* is further complicated by its seasonal distribution in different areas. South of cape Cod it occurs at Woods Hole as one of the dominant late summer and autumn species, and is commonly found at this time offshore as far south as Chesapeake bay (Bigelow 1926, p. 221). This, together with the fact that it has not been reported north of cape Sable, would tend to group it with the southern ranging Virginian fauna, were it not that propagation immediately south of cape Cod apparently takes place at minimum temperatures in January and February (Fish 1925, fig. 44) and, as a typically winter form in Chesapeake bay (Wilson 1932b, p. 23), it is probable that winter spawning occurs there also. Considering again its success in maintaining itself in the gulf of Maine where it usually reaches its peak at approximately the same time as at Woods Hole, it seems likely that *C. typicus* is really a boreal-temperate species which is more indifferent to high temperatures than the more typical boreal forms.

Regional variation. All boreal species vary considerably in abundance in different parts of the region. This is to be expected where variability in the productivity of different areas is so great. Certain species, particularly the dominant ones, may swarm over large areas, as in the case of *Calanus* in the western basin in summer. Bigelow (1926, p. 18) obtained six quarts of this species with many larval *Merluccius* and little else in a 15-minute metre net haul in the upper 40 metres off cape Cod on July 22, 1916. Again on June 26, 1934, a 15-minute oblique haul with a half-metre net of number 15 silk bolting cloth yielded one quart of *Calanus* with only an occasional *Limacina* offshore in the western basin. No such aggregations of this species were found in the inner gulf or bay of Fundy at any time in 1931 or 1932.

Strictly local swarms of individual species are also common. In some instances these concentrations occur regularly, particularly in the vicinity of offshore banks in summer, and are probably due to localized production on a relatively large scale. Bigelow has described repeated observations of concentrations of *Sagitta elegans* and *Temora longicornis* on Georges bank in July and August, and *Euthemisto* on Browns bank in midsummer (1926, pp. 21-22). In August, 1926, *Temora* again dominated in collections from the central portion of Georges bank, and on September 20, 1932, spawning adults of *Euthemisto compressa* formed 26.2 per cent of the haul at one station (A1400) off the inner edge of this bank

but did not exceed 2 per cent at any of five other stations in the same general area (fig. 22).

Except in the vicinity of restricted production centres, local swarms of endemic boreal species appear to result most commonly from a combination of environmental factors which make their location largely a matter of chance. Such concentrations are usually of limited duration and their location unpredictable. A local swarm of *Sagitta elegans* in the bay of Fundy, forming 42.9 per cent at sta. 9 and 33.8 per cent at sta. 10A on April 19, is an example of this type of swarm (fig. 23).

FIGURE 22. Zooplankton population dominated by *Euthemisto compressa* at station A1400 on September 20, 1932. Eggs and larvae, visible in figure, are from the brood pouches.

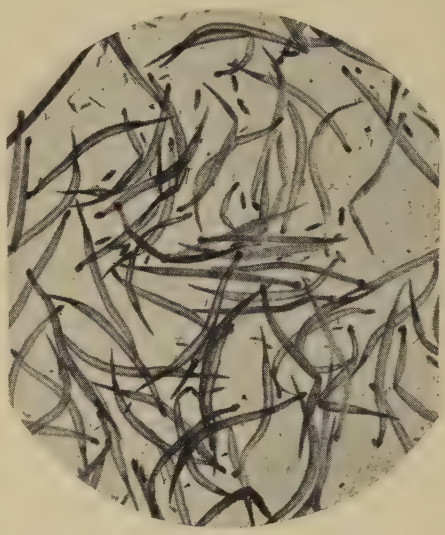

FIGURE 23. Zooplankton population dominated by *Sagitta elegans*. Bay of Fundy (station 9), April 19, 1932.

To cite another example, on May 24 *Oikopleura labradoriensis* formed 20 per cent of the population at sta. 33 in the central area, but less than 1 per cent at neighbouring stations on either side. Similar local swarms of this species were found at several other stations in the eastern gulf and bay at this time.

Certain species appear to be constant residents in some localities and distinctly seasonal in others. *Pleurobrachia pileus* was invariably found abundant by Bigelow (1926, p. 367) in the region of German bank and the shoals west of Nova Scotia, and the following records of its occurrence in 1932 at all stations in this locality affords added confirmation.

1932	Station	Percentage
Jan. 22	N 52	92.5
Jan. 22	N 54	27.8

1932	Station	Percentage
Jan. 23	N 55	87.8
Jan. 23	N 56	42.4
Jan. 25	N 58	71.9
April 20	N 190	70.7
April 24	N 200	66.6
April 24	N 201	92.5
May 14	N 244	4.8
Sept. 23	A 1410	5.7

Elsewhere this species appears to have a definite seasonal periodicity in its annual cycle as described on page 299.

Evaluation of species. In determining the relative numerical importance of individual species of the endemic boreal group, local irregularities in distribution have been overcome by taking the average of all stations in the area. Young stages when found in the metre net have been included in the calculations. Particularly in *Clione, Euthemisto,* and *Meganyctiphanes,* juveniles often comprised the greater part of the count.

With the exception of euphausiids the boreal population appears to have been effectively sampled. The fact that the largest numbers of *Meganyctiphanes norvegica* and the several species of *Thysanoessa* were regularly taken at night, however, indicates clearly that an appreciable part of this stock successfully avoided the nets during the daylight hours. The abundance of eggs during the breeding season affords further evidence of a richer population than our daytime captures would indicate. It should also be remembered in this regard that the present method of analysis deals solely with numerical importance. Euphausiids, because of their large size frequently formed the bulk of a sample even though outnumbered by several smaller species. They undoubtedly have a very important part in the natural economy of the region, and will be considered later in a separate publication.

Bay of Fundy. For the year October 1931 to September 1932 the following relative percentages (by number) were obtained. Records for *Oithona similis* and *Microsetella norvegica* are available only for the period April-September and will be considered later, p. 242.

Calanus finmarchicus	38.6	*Oikopleura labradoriensis*	0.5
Centropages typicus	22.6	*Thysanoessa sp. (juvenile)*	0.3
Pseudocalanus minutus	10.0	*Oithona plumifera*	0.2
Euphausiid eggs	8.9	*Limacina retroversa*	0.2
Metridia lucens	7.1	*Thysanoessa inermis*	0.1
Sagitta elegans	2.2	*Euthemisto compressa*	0.1
Tomopteris catherina	1.0	*Temora longicornis*	0.1
Stephanomia cara	1.0	*Halithalestris croni*	0.04
Meganyctiphanes norvegica	0.7	*Euchaeta norvegica*	0.04
Clione limacina	0.7	*Thysanoessa neglecta*	0.01

Thysanoessa raschii	0.01	*Euthemisto bispinosa*	T
Fritillaria borealis	0.01	*Hyperia galba*	T
Aglantha digitalis	0.01	*Pleurobrachia pileus*	T
Anomalocera patersoni	T	*Beroë cucumis*	T
Thysanoessa longicaudata	T		

The four most important boreal species in the bay, *Calanus, Centropages, Pseudocalanus,* and *Metridia,* comprised 78.3 per cent of the total zooplankton population in 1931-32, and in 1917, when the *Centropages* autumn crop apparently failed to develop (0.1 per cent), the percentage of the other three species was proportionately greater, amounting as previously stated (p. 236) to 90.1 per cent. Euphausiid eggs, although strictly seasonal, form a surprisingly large percentage, and may themselves prove a very important source of food for certain species.

In 1931 the average for all stations in August and September in the bay indicates that the same six boreal forms and those alone exceeded one per cent. The results for this period in the two years are listed below.

	1931	1932
Calanus finmarchicus	49.1	35.6
Centropages typicus	7.4	26.0
Metridia lucens	2.3	10.0
Pseudocalanus minutus	3.9	4.2
Meganyctiphanes norvegica eggs	28.6	8.7
Sagitta elegans	2.2	1.6
	93.5	86.1

TABLE VII. Occurrence of boreal zooplankton in

Area	Total region						Western area			
Month, 1932	Apr.	May	June	Aug.	Sept.	Apr.–Sept.	Apr.	May	June	Aug.
Cruise	26	27	28	30	32		26	27	28	30
Calanus finmarchicus	25.4	58.4	42.9	39.3	56.7	44.5	34.6	68.0	40.0	40.7
Metridia lucens	5.3	6.5	26.3	20.1	11.6	14.0	6.9	11.0	38.0	15.9
Pseudocalanus minutus	13.1	11.7	15.1	2.2	1.3	8.7	10.8	4.3	3.5	..5
Centropages typicus	T	.1	.1	10.3	25.9	7.3	T	.08	.3	10.9
Euphausiid egg	21.2	8.6	9.4	9.7	.2	9.8	33.1	5.9	10.6	8.3
Sagitta elegans	5.9	.8	.4	1.1	.5	1.7	.9	T	.3	.8
Meganyctiphanes norvegica	1.8	.9	.5	5.0	.02	1.6	1.6	2.3	.7	12.3
Oikopleura labradoriensis	.6	4.4	.6	.4		1.2	1.5	5.5	.5	.6
Limacina retroversa	.2	.07	.6	2.2	.4	.7	.3	.2	.7	4.7
Tomopteris catherina	2.0	.2	.03	.2	.03	.5	.2	.07	T	.5
Thysanoessa sp. (Juvenile)	.07	1.6	.8	.01	T	.5	.2	.8	.9	T
Stephanomia cara	.8	.2	.3	.5	.07	.4	1.6	.5	.4	.9
Clione limacina & young	1.3	.3	.03	.1	.03	.4	1.5	.02	.03	.1
Euchaeta norvegica	.3	.2	.01	.04	.3	.2	T	.7	.6	.04
Temora longicornis		.03	.02	.2	.2	.1			.06	
Fritillaria borealis	.5	.07	T	T		.1	1.9	.04	T	T
Aglantha digitalis	.04	.01	.03	.2	T	.06	.03	.02	.04	.3
Thysanoessa inermis	.2	T	T	.05	T	.05	.01	T	T	.04
Euthemisto compressa & young	T	.04	.01	.1	.1	.04	T	.02	T	.2
Anamalocera patersoni			T	.01	T	T			T	..02
Halithalestris croni	T	T	T			T	.01			
Euthemisto bispinosa	T				T	T				
Hyperia galba	T	T	T	T	T	T	T			
Thysanoessa longicaudata	T	T		T	T	T	T			
Thysanoessa neglecta	.02	T	T	T	T	T	T	T	T	T
Thysanoessa raschii	T	T	T		T	T	T		T	
Beroe cucumis	.02	T				T	T			
Pleurobrachia pileus	T	T		.05		.01				.1

Observations were made about two weeks later in 1932 than in the previous year, which would account for the greater augmentation of *Centropages typicus* and decrease in *Meganyctiphanes* eggs. Except for *Metridia lucens,* which was generally more abundant throughout the region in 1932 than at a comparable period in the late summer of 1931, the composition of the population would appear to have been substantially the same during the two years.

Total region. Comparing all areas, table VII indicates that members of the boreal group occurred throughout the region and in very much the same relative proportion in 1932.

During the period from April to September certain species, more restricted to offshore waters, were relatively less abundant in the turbulent eastern coastal area, thus increasing somewhat in those areas the relative importance of the more universal species. This is evident in the case of *Metridia lucens* where the mean decreased gradually from 19.4 per cent in the western gulf to 6.9 per cent in the bay while the percentage of *Pseudocalanus* increased to the eastward over the same range from 3.9 per cent to 16 per cent. However, when combined, the totals for the four dominant species were very similar, declining but slightly from 76.8 per cent west of Mount Desert to 74.1 per cent in the central area and 72.6 per cent in the bay. Considered by months, these four species totalled throughout the region 43.8 per cent in April, 76.7 per cent in May, 84.4 per cent in June, 71.9 per cent in August and 95.5 per cent in September, or 74.5 per cent for the season.

Averaged from the five cruises between April and September, forming the period of greatest divergence in the zooplankton, but seven boreal endemic species exceeded one per cent in the western gulf, and five in the other two areas. This

1932. Relative percentages in metre net collections

		Central area						Bay of Fundy					
Sept.	Apr. –	Apr.	May	June	Aug.	Sept.	Apr. –	Apr.	May	June	Aug.	Sept.	Apr.–
32	Sept.	26	27	28	30	32	Sept.	26	27	28	30	32	Sept.
43.2	45.3	18.5	54.9	39.0	42.7	90.2	49.1	23.2	52.2	49.7	34.4	36.8	39.3
25.4	19.4	4.0	6.0	34.2	31.6	2.3	15.5	5.0	2.5	6.8	13.0	7.1	6.9
.3	3.9	5.2	12.5	11.8	1.4		6.2	23.2	18.4	30.1	4.7	3.6	16.0
29.7	8.2			.1	8.4	7.5	3.2			.02	11.6	40.4	10.4
T	11.6	27.2	11.9	11.3	4.0		10.9	3.4	8.1	6.2	16.8	.5	7.0
T	.4	1.0	.3	.4	.9	T	.5	15.9	2.0	.5	1.7	1.4	4.3
T	3.4	.03	.3	.4	1.8	T	0.5	3.8	.2	.4	.9	.05	1.0
	1.6	.2	4.7	.1	.4		1.1	.1	3.1	1.1	.1		.9
.3	1.2	.2	T	.6	2.6	T	.7	.1	.03	.6	.8	.7	.4
T	.2	.5	T	T	.1	T	.1	3.8	.3	.06	.1	.1	.9
T	.4	.04	1.2	.7	T	T	.3	T	2.3	.8	.03	T	.6
T	.7	.8	.05	.3	.4		.3	.3	.2	.1	.3	.02	.2
T	.3	.8	.03	.1	.06	T	.2	1.5	.5	T	.07	.1	.4
.7	.5	.6	.1	.07	.06	T	.2	.02	.1	.01	.02	.02	.03
.2	.05				.04		.01		.06	.01	.5	.5	.2
	.4	.1	.07	.4	T		.1	T	.08		T		.02
T	.08	.04	T	.05	.3		.08	.04	T	T	.05	T	.02
T	.01	.01	T	T	.1	T	.02	.5	T	T	.02	T	.1
T	.04	T	T	.02	.2	T	.04	T	.1	T	.03	.3	.09
	T			T	.02		T				T	T	T
	T	T	T				T	T	T	T			T
T	T					T	T	T					T
	T		T	T			T	T	T	T	T	T	T
	T	T			T	T	T	T	T		T		T
	T		T		T	T	T	.05	T	T	T	.01	.01
	T	T					T	T	T	T		T	T
	T	T					T	.05	T				.01
	.02	T			.05		.01	.03	T		T		.01

accords very closely with the record of six species in the bay for the year 1931-32, and four in 1917. *Calanus finmarchicus* never failed to exceed all other species in the monthly averages for all areas except in April in the bay when it was equalled by *Pseudocalanus*. However, in the western area in June it was but two per cent more numerous than *Metridia lucens*.

Two endemic boreal copepods, *Oithona similis* and *Microsetella norvegica*, because of their small size, could not be sampled in a representative manner with coarse metre nets. Both, however, were taken effectively in the fine nets and with the pump, and although these data are limited to the upper 50 metres, the two species are known to have their centre of abundance within that range in the present region in summer. The following table gives the mean abundance of adults in the total region between April and September in 1932, and for the two months August and September in 1931.

	April-June	August-September	
	1932	1932	1931
Oithona similis	2262	1941	1822
Microsetella norvegica	193	555	153

April-June results show the number per minute of towing; August-September, the number per cubic metre. Unfortunately, due to different methods used, it was not possible to determine the relative abundance of microcalanids and macrocalanids (adults). A comparison of some of the young in the total region is shown below, but cannot be considered even suggestive of the position of the adults in the quantitative scale of species, for as previously described (Fish 1936b), the degree of mortality in developmental stages apparently varies greatly in different forms.

	April-June	August-September	
	1932	1932	1931
Oithona similis	5,316	19,057	19,375
Microsetella norvegica	6	666	478
Calanus finmarchicus	3,729	509	2,022
Pseudocalanus minutus	13,304	4,573	12,735

Oithona, in which such a relatively minute percentage of the young reach maturity (Fish 1936c, p. 185), occupies at certain periods a dominant position in the scale of plankton larvae, but the adults have rarely been reported to form a significant part of the population except perhaps in restricted localities for short periods. The latter condition was also found in *Microsetella*, which in 1931 and 1932 was far less abundant than *Oithona*, but in 1930 swarmed during July and August in Frenchmans bay, outnumbering both adults and young of all other zooplankton species combined.

Rotifers were not represented in the coarser net collections, but the fine net and pump records showed them to be extremely abundant in certain localities, particularly during the late summer. In all four species were found: *Synchaeta johanseni, S. triophthalma, Trichocerca curvata,* and *Northolca foliacea*. For

identifications of these species we are indebted to Mr. Frank J. Myers, who examined specimens taken in Frenchmans bay by the senior author in 1930. As no previous list of marine rotifers in the gulf has been published we may add the following species recorded by Mr. Myers from Frenchmans bay, although the greater part is no doubt restricted to the immediate vicinity of the shore line.

Colurella ambleytela (Gosse). From algae clinging to the laboratory dock.
Encentrum eristes Harring and Myers. From *Fucus,* alongshore, Laboratory point.
Encentrum marinum (DuJardin). From *Fucus,* alongshore, Laboratory point.
Encentrum nesites Harring and Myers. From *Fucus,* alongshore, Laboratory point.
Lecane grandis (Murray). Tidepools near Sand point. Northern shore.
Notholca foliacea (Ehrenberg). Limnotic variation. Towings off Porcupine Is.
Proales neapolitana (Daday). From algae clinging to laboratory float.
Proales reinhardti (Ehrenberg). From algae clinging to laboratory float.
Proales similis (deBeauchamp). From *Fucus,* shore, Laboratory point.
Synchaeta baltica (Ehrenberg). Towings near Laboratory point.
Synchaeta johanseni Harring. Towings off Porcupine island.
Synchaeta triophthalma Lauterborn. Towings off Porcupine island.
Trichocerca curvata (Levander). Towings off Porcupine island.
Trichocerca marina (Daday). From *Fucus,* shore, Laboratory point.

Synchaeta johanseni was the dominant rotifer both in 1931 and 1932 in the open gulf and bay of Fundy, and in 1930 in Frenchmans bay. Regarding this species Mr. Myers wrote: "This is only the second time reported. Harring described this species from poor material sent him by F. Johansen from station 36, off Cape Lyon, in Amundsen Gulf, Alaska. Harring said that the form and position of the eyespot could not be made out from his material. Fortunately your material is fine and clears up all doubts about the eyespot; one large at posterior tip of ganglion and two accessory spots higher up in the head." In 1932 it was observed in the Quoddy region in April and by May was distributed in small numbers as far west as Penobscot bay. The seasonal maximum occurred in June west of Mount Desert, and in August in the central area and bay of Fundy, as shown in the following table.

TABLE VIII. Regional variation in abundance of *Synchaeta johanseni*. Net collections, April-June; pump collections, August-September

1932	Number per minute			Number per cubic metre	
Section	April	May	June	August	September
Casco bay	0	0	1549	377	..
Penobscot bay	0	368	2734	1,507	..
Mount Desert	0	795	0	320	..
Moose Peak	0	21	0	7,073	..
Passamaquoddy bay	29	110	560	15,052	0
Pt. Lepreau	0	214	0	12,491	0
Cape Spencer	0	300	T	4.146	10

There was at all times marked regional variation, with numbers reaching 31,687 per cubic metre in 1932 when propagation was centred in the northeastern part of the region around Grand Manan (fig. 24).

Trichocerca curvata ranked second in importance among the rotifers. In April (1932) none were found in the inner gulf or bay of Fundy but in the outer gulf small numbers appeared at one station in the western channel, two along the

FIGURE 24 (part)

west coast of Nova Scotia, and four off the south coast. In May a few were taken at the outermost station off Penobscot bay (sta. 29) and on the Nova Scotian side of the bay (sta. 9A). In June it was found only in Passamaquoddy bay. The maximum occurred in August after which a rapid decline must have taken place, for none were obtained in September. In 1931 small numbers, up to 565 per cubic metre, were taken at three stations in the gulf and bay in August, but not at five stations in the bay the following month. Like *Synchaeta, Trichocerca* was cen-

tred in the vicinity of Grand Manan in August (fig. 24) and never appeared in appreciable numbers west of Mount Desert.

Synchaeta triophthalma occurred sparsely in the eastern part of the region in August and September of the two years. *Notholca foliacea* was not found in the gulf in 1931 or 1932, but in the bay a single specimen was taken at one station (11A) near shore in April and up to 565 per cubic metre at five stations in the

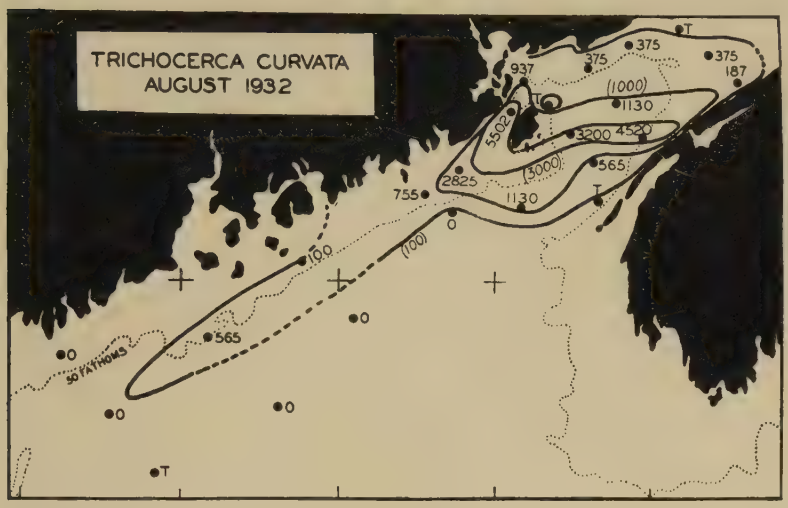

FIGURE 24 (con.). Distribution of dominant rotifers. Number per cubic metre.

inner bay in August. In 1930 a few individuals of both of these species were obtained in Frenchmans bay in August.

Although small in size rotifers may be important as food for plankton feeders in turbulent areas during the summer months. It is to these regions of violent mechanical mixing, particularly about Grand Manan, where minimum numbers of other planktonic species occur, that this group is largely restricted.

A similar condition was observed in Frenchmans bay in 1930. There *Synchaeta johanseni,* although swarming in the warmest season, was centred in the region of most violent mixing, the channel between Porcupine and Iron Bound islands. *Trichocerca curvata* was also found only in this locality in 1930.

It would appear that rotifers develop very rapidly and survive for so short a period that they do not become very widely dispersed, and like diatoms local concentrations may be considered indicative of production centres. All species reached a maximum in August.

OCEANIC IMMIGRANTS

Immigrant species, the means by which they reach the gulf of Maine, their seasonal variation and dispersal within the region, have been so fully described by Bigelow (1926, pp. 51-69) that little need be added except an evaluation of

their relative importance in the local population during the period of the present investigations.

Contributions from outside waters consist of six general classes: (1) endemic species transported as juveniles in the surface drift or entering later with the large volume of mixed water from the outer part of the continental shelf; (2) non-endemic or partially-endemic species like *Metridia longa* and *Calanus hyperboreus* whose centres of abundance lie in neighbouring regions to the north, and which depend largely, if not entirely, upon contributions from outside waters for the local stock; (3) non-endemic or partially-endemic species, as *Sagitta serratodentata* and *Paracalanus parvus,* from neighbouring regions to the southward; (4) arctic immigrants, like *Limacina helicina,* entering from the Nova Scotian current; (5) tropical migrants originating in the Gulf Stream (*Salpa* and *Phronima*), and (6) deep water forms entering with the cold bottom influx through the eastern channel (*Sagitta maxima* and *Diphyes arctica*).

The greater part of all zooplankton forms entering the gulf throughout the year are endemic boreal species, but an evaluation of their importance cannot be made with available data as they are indistinguishable from the local stock and their abundance and distribution beyond the confines of the gulf have not been sufficiently well determined. Differences in the periods of propagation, if indeed they occur, would make possible a detection of young stages passing into the gulf, but there seems little possibility of calculating effectively the augmentation by adults.

The remaining classes, for present purposes, have been combined in two groups and designated as northern or southern, depending on whether they originate in colder or warmer water than that characterizing the region of the gulf and bay of Fundy.

Northern group. The following seven northern forms were taken within the gulf during the two years: *Metridia longa* and *Calanus hyperboreus* (northern); *Limacina helicina, Aetidius armatus* and *Scolecithricella minor* (arctic); *Sagitta maxima* and *Diphyes arctica* (deep water). *Hyperoche tauriformis* has frequently been taken in the region, and averaged 2.4 per cent of the population at four stations off the south coast of Nova Scotia on January 21, 1932, but did not appear in any of our collections from the gulf or bay of Fundy. To these may be added the following species, classed as northern, which were absent in present collections but have previously been reported from the gulf (Bigelow 1926, p. 598): *Ptychogena lactea, Mertensia ovum, Oikopleura vanhöffeni, Scaphocalanus magnus, Chiridius armatus, Chiridius obtusifrons, Gaidius brevispinus, Gaidius tenuispinus, Heterorhabdus norvegicus,* and *Scolecithricella ovata.*

Another species, *Clione limacina,* assigned to the northern group by Bigelow (1926, p. 61), has been included with local boreal species in the present arrangement because, although its centre of abundance lies in more northern waters, it more closely approaches the endemic stock than the members of the northern group. The numbers of young in all stages of development in the gulf and bay both in 1931 and 1932 were more than sufficient to account for the local adult

stock, and would indicate that the species is endemic at least as far south as cape Cod, and probably farther. Dr. Mary Sears has informed us that she has found early and late developmental stages in large numbers over a wide area south of the cape, and in 1922 and 1923 we obtained occasional early larvae at Woods Hole. Dr. Huntsman (Bigelow 1922, p. 134) also reported larvae widespread throughout the region from the gulf of Maine to the gulf of St. Lawrence, but not in estuaries. However, a significant part of the stock of *Clione* and also of *Tomopteris catharina* is probably derived from more prolific areas north of the gulf. The latter species occurred throughout the year 1931-32 in the bay of Fundy, appearing in all stages of development, but Bigelow has found evidence that it fails to reproduce successfully in the gulf in certain years (1926, p. 68). Large local swarms of either species would be considered indicative of immigration.

Evaluation of species. Northern species in the bay of Fundy averaged for the year October 1931 to September 1932 as follows: *Metridia longa* 0.2 per cent, *Calanus hyperboreus* 0.03 per cent, *Sagitta maxima* T, *Limacina helicina* T, *Diphyes arctica* T, and *Aetidius armatus* T. *Scolecithricella minor* appeared in September, 1931, but was not found in 1932. In 1917 no typically arctic species were observed but northern species were relatively more important than in 1931-32. In the former year *M. longa* attained a maximum of 2.9 per cent in the bay in February, and averaged 0.9 per cent for the year. *C. hyperboreus* averaged 13.4 per cent in June, 2.5 per cent in July and 1.8 per cent for the year. *M. longa* occurred in the bay in every month both in 1917 and in 1931-32. *C. hyperboreus* was lacking in collections in April, 1917, and from December to March in the latter year. It might be suggested from these data that the small stock of *C. hyperboreus* in the bay tends to become depleted in the late winter and early spring and is in some instances exhausted before vernal restocking from outside waters takes place. Observations by Willey (1921, p. 191) indicate that late copepodite stages surviving the winter in the bay complete their metamorphosis, although he did not report any females with eggs, and no nauplii were found in the course of the present investigations.

The following mean values for the total region during the period from April to September, 1932, are very similar to those for the year in the bay: *M. longa* 0.1 per cent, *C. hyperboreus* 0.04 per cent, *S. maxima* T, *L. helicina* T, *D. arctica* T, and *A. armatus* T. Considered by areas, the central area corresponded very closely with the bay, but west of Mount Desert *M. longa* was not taken after April, and *C. hyperboreus* occurred at but one station after June. This agrees with Bigelow's finding that "Evidently the numbers of *C. hyperboreus* existing in the gulf increase considerably from February to May and then decrease during June, while none at all have been detected at most of the midsummer and autumn stations." (1926, p. 215.)

Sagitta maxima enters the gulf throughout the year in the cold bottom water (Bigelow 1926, p. 327) and in 1932 was found widespread in the region at seven stations in April, five in May, eleven in June, twelve in August, and four in Sep-

tember. In the bay of Fundy it also occurred in September, October, and December 1931, and in January and March 1932.

Typically arctic forms were found by Bigelow (1926, pp. 60-61) in greatest abundance and most widespread in May, being closely associated with the seasonal

FIGURE 25 (part)

expansion of the Nova Scotian current. Variations take place from year to year, however, and in 1932 the first arctic species, *Aetidius armatus,* appeared at the outermost station (sta. 29) in one of the western sections on May 30. Another specimen of this species was obtained in the bay of Fundy (sta. 10A) in August.

Limacina helicina (sta. 10A) and *Diphyes arctica* (sta. 11A) were found at adjoining stations in the inner bay on June 21, the latter also occurring at sta. 33 in the central area and later at five widely separated stations throughout the region in August. In 1931 *Scolecithricella minor* was taken in the bay in September.

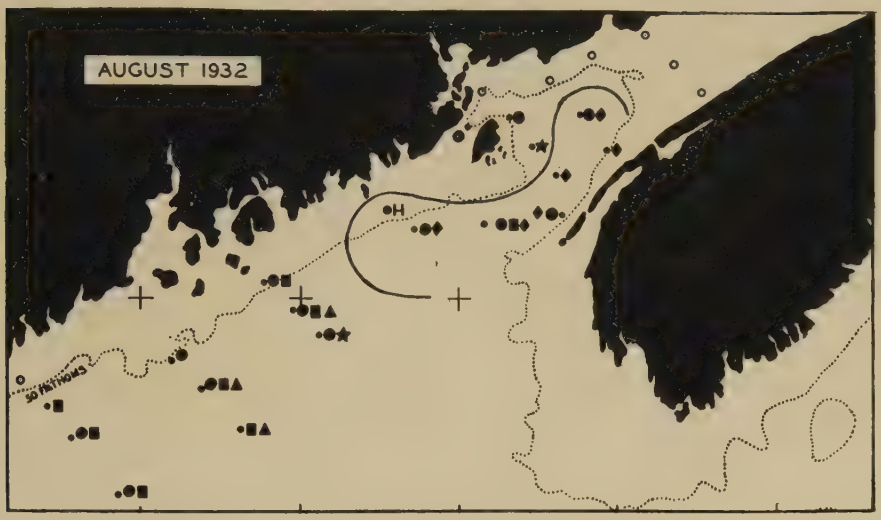

FIGURE 25 (con.). Distribution of tropical species.

Except as indicators, arctic immigrants are of little value in the region and usually appear as single individuals in the hauls. The northern forms *M. longa* and *C. hyperboreus* and the deep water species *S. maxima* regularly occur in somewhat greater abundance but they, too, are rarely present in significant quantities over the region as a whole. *M. longa* reached 4.8 per cent on one occasion (sta. 12 in April) and *C. hyperboreus* at sta. 7 in May amounted to 1.6 per cent, but the average for the region in each instance in 1932 did not exceed 0.3 per cent. *S. maxima* also formed 4 per cent of a haul in the deep basin at the entrance of the bay in January 1932, but occurred at only two other stations out of 43 in the region that month. All of these concentrations were observed in the bay where the numbers of immigrants tend to loom proportionately larger than elsewhere in the region because of the small local zooplankton population.

Southern group. Unlike the northern group, of which almost all of the pelagic species found in the arctic drift have on occasions been taken well inside of the gulf, a relatively small fraction of the Gulf Stream population penetrates far shoreward of the outer banks. Almost any of the myriad of tropical surface species may be expected along the south side of Georges bank, but year after year only the same comparatively few species appear to survive sufficiently long in boreal waters to become very widely distributed. Even so the number of species far exceeds those from the north.

In 1931-32 the following ten species were found in the inner coastal area:

Candacia armata, Cymbasoma rigidum, Eucheirella rostrata, Heterorhabdus spinifrons, Pleuromamma robusta, Phronima sedentaria, Rhincalanus nasutus, Salpa fusiformis, Salpa zonaria, and *Sagitta serratodentata.* In September 1932, six additional southern species were obtained offshore in the vicinity of Georges bank: *Corycaeus elongatus* (sta. A1415), *Nematoscelis megalops* (A1400, A1412, A1413), *Sagitta inflata* (A1415, A1416), *Ocypoda albicans* megalops (A1413, A1414), *Odontodactylus sp.* larvae (A1414), and *Thysanoessa gregaria* (A1414).

It seems probable that *Paracalanus parvus* should be included with the southern group in the western Atlantic because its centre of abundance is certainly located south of cape Cod (Wilson 1932a, p. 39, 1932b, p. 26), and, although it appears to propagate successfully and become fairly numerous in the gulf in some years (Bigelow 1926, p. 267), it is almost if not entirely absent in others. Young stages were found in September 1931 and from April to September in 1932, indicating the presence of a very small adult stock, but they were so sparse that not one individual appeared in the metre net collections of the two years or in those from the bay of Fundy in 1917.

Tropical communities enter the gulf sporadically during the summer, usually between April and September, and successive waves may be composed of quite different associations depending on the nature of the stock in the Gulf Stream at the time. Thus in April 1932 (fig. 25) four tropical species, *Rhincalanus nasutus, Pleuromamma robusta, Candacia armata,* and *Cymbasoma rigidum,* were found restricted to the eastern gulf and the drift into the bay of Fundy. By mid-May *Eucheirella rostrata* appeared and ranged from the eastern channel around the margin of the gulf to Penobscot bay and well into the bay of Fundy. By this time *Rhincalanus* had advanced at least as far west as Casco bay. A second wave of immigrants (fig. 25), dominated by *Salpa fusiformis,* appeared in August with a distribution corresponding closely with that of the former group in April. Of the earlier migrants only *Eucheirella* and *Pleuromamma* remained in the bay and *Rhincalanus* in the central coastal area (Mount Desert and Penobscot bay sections). In September observations, including the outer gulf, indicated conditions over much of the region similar to the inner gulf in August, except that *Phronima* occurred at one station in the central area, all stations along the inner edge of Georges bank, and one on the bank. A second influx of *Rhincalanus* was found in the drift entering the bay of Fundy on September 15-16. A September invasion of *Pelagia noctiluca,* observed for the first time in Canadian waters, was reported in 1934 (Leim and Hachey 1935, p. 280).

In the case of the genus *Salpa,* one of the most typical of the tropical migrants, it is not known whether the stock in the Gulf Stream is so completely dominated by one species at a time as would be inferred from the distribution of immigrants in boreal waters. So far there is no record of two species occurring in the gulf at the same time, even though successive invasions during a season may be composed of different species. Of five species taken by Bigelow in the Gulf Stream south of cape Cod in 1913, only one, *S. tilesii,* was reported from the gulf. In 1931, *S. zonaria* appeared in mid-September along the Nova Scotian side of the

bay, and a few weeks later entered the Quoddy region. In the vicinity of St. Mary bay (fig. 25) it remained throughout the autumn and formed 24 per cent of the population at one station (N40) in January 1932. *S. fusiformis* appeared in August (1932) in the eastern gulf, and was later found on the southern part of Georges bank in September (sta. A1415). Again in June 1934 collections from the region of Georges bank yielded a large number of *S. zonaria,* while a half metre oblique net haul in the same region in August yielded over three quarts (2.8 litres) of *S. democratica-mucronota* in 15 minutes. Other similar occurrences in the gulf have been described by Bigelow (1914a, p. 121; 1917, p. 245; 1926, pp. 56-57), in each instance the *Salpa* stock being composed of one species. Subjected to uniform mechanical action and evidently able to survive equally well in boreal waters during the warm season, one would expect the species of *Salpa* entering the gulf to be in much the same relative proportion as in adjacent ocean waters. Pending acquisition of the necessary data, it would appear logical to conclude that wide seasonal fluctuations in abundance do occur within the Gulf Stream, as suggested by Bigelow (1909, p. 199), and that immigrants in the gulf are indicative of the particular species dominating at the time.

Evaluation of species. In the bay of Fundy average values of southern forms for the year 1931-1932 were negligible. *Sagitta serratodentata,* the most important species with a yearly mean of 0.04 per cent, amounted to only 0.2 per cent of a scanty population when it occurred in greatest abundance in March. It was found, however, in every month except October, January, and possibly February (collections destroyed by fire). In 1917 it appeared in but one haul, in November. Seven tropical species occurred as traces in the bay in 1931-32; *Candacia armata* (June, September, November, December), *Cymbasoma rigidum* (June), *Eucheirella rostrata* (May, June, August, September), *Pleuromamma robusta* (August, September), *Rhincalanus nasutus* (June, August, September), *Salpa fusiformis* (August 1932), and *Salpa zonaria* (September, November, December in 1931, and January 1932).

Values for the total region between April and September 1932 were of the same general order. *S. serratodentata* averaged 0.03 per cent in the western area, 0.04 per cent in the central area, and 0.02 per cent for the entire gulf and bay. All other species occurred as traces. The central area yielded the largest number of species (eight) and the western area the smallest (four).

NERITIC SPECIES (IN OFFSHORE WATERS)

The term neritic should rightly apply to all forms associated with the coast or shallow waters, and neritic plankton would include true planktonic species, pelagic fish eggs and larvae, and the pelagic eggs and larvae of benthonic coastal species. In the present analyses, these three classes have been evaluated separately and the term "neritic species" restricted to those coastal forms which are pelagic as adults. In the region of the gulf of Maine this group is composed of copepods, Cladocera, and Medusae.

In all, 26 neritic species were obtained during the period of the present investigations. Of these seven were copepods, three Cladocera and sixteen Medusae.

With the exception of two species, *Acartia bifilosa* and *Thalestris longimana,* which were found only within bays in the western and central areas, all of the species were at some time taken within the range of the routine offshore stations. Four species, *Podon polyphemoides, Podocoryne carnea, Steenstrupia virgulata,* and *Tiaropsis diademata* reported in 1931 did not appear in the collections of the second year.

It is probable that few additions will be made to the list of neritic Crustacea (excluding benthonic species) found in offshore waters of the gulf, but our records of Hydromedusae are far from complete. Occurring frequently for very short periods at the surface, they are easily missed on monthly cruises.

All boreal neritic species appear to be seasonal in the plankton and pass a portion of the year at the bottom. Some, like the Hydromedusae, remain as active organisms in the benthonic state while others (Entomostraca) have a resting stage, usually in the form of winter eggs. In this respect they resemble fresh water populations (excluding marine relics) and quickly disappear when unfavourable environmental conditions are encountered. The boundaries of their normal geographical range are thus much more clearly marked than those of the offshore population. An alongshore drift further assists in retaining neritic forms in the immediate vicinity of the coast over much of the gulf, but the increasing percentage of this group encountered upon approaching the outer headlands from offshore indicates that considerable quantities are constantly drawn seaward in the general circulatory drift. Particularly in the productive sector from Penobscot bay to Casco bay, adequate means of transportation almost directly offshore are provided as soon as the narrow band of alongshore drift has been traversed (through tidal action), and, were it not for other limiting factors, neritic species would become widely distributed over the basin in a very short time. However, like stream species restricted to the immediate vicinity of outwash into lakes (Fish 1929, fig. 77), Bigelow (1926, pp. 32 and 36) rarely found the neritic population of the gulf more than a few miles offshore.

The regional distribution in 1931 and 1932 accords very well with previous observations. In the gulf of Maine, for the period April to September in 1932, neritic zooplankton formed but 0.5 per cent of the population in the western area, and 0.7 per cent in the central area (table IV). Data from other parts of the gulf in May indicated neritic species forming 0.6 per cent off cape Ann, 0.2 per cent in the central part of the western basin, and absent in the central basin, eastern channel and Browns bank. Again in September traces were found in the western area and outer gulf (off the inner margin of Georges bank), but not in the central area, Georges bank, or the west coast of Nova Scotia (table VI).

The change in the composition of the population upon approaching the coast is illustrated in the records of August during the two years. In 1931 stations were taken on a line roughly paralleling the coast and, with two exceptions, within the 100 metre contour (fig. 1), seven of the eleven stations in the gulf being well

inside of the area covered during the following year. Neritic species in the two regions of the inner gulf yielded the following mean values:

August	*Western area* (per cent)	*Central area* (per cent)
1931	27.0	15.6
1932	1.3	3.1

Even at the innermost stations (excluding bays) members of the open gulf population did not fall below 63 per cent during the two years.

In the bay of Fundy the zooplankton was found to be somewhat more neritic in character than in the gulf, although the mean for the year October 1931 to September 1932 amounted to only 1.9 per cent. A slight summer increase over the western area was noticeable east of Mount Desert and the percentage rose still higher in the bay (table IV). The larger values in the eastern region were, however, due more to the small stock of offshore boreal forms than to an actual increase in the number of neritic species, as is indicated by the volumes in the different areas at this time (figs. 16 and 17). The mean in the bay for the period July-September in 1931 was 5.6 per cent and in 1932, 5.9 per cent. The same three forms, *Acartia, Evadne,* and *Phialidium* dominated the neritic stock throughout the entire region at this time. At other times during the year the monthly average in the bay did not exceed 0.7 per cent (table V).

Available records indicate that north of cape Cod the neritic community is for the most part a summer one, having its origin in April and termination in October. The greater part of the neritic species in 1931-32 did not appear before May or after September in the bay of Fundy. But one exception was observed during this period: *Acartia longiremis* occurred sporadically in small numbers throughout the year. In 1917, however, it was taken only in April. During the colder months open gulf species populate the entire region including inshore waters. With vernal warming neritic species become numerous first in the more shallow bays, and, except in deeper areas where low bottom temperatures persist, may largely replace the winter stock in inland waters. There follows a progression of seasonal changes in the neritic population as new forms appear and others decline until autumn. At this time in 1931 the summer stock, at least in the bay of Fundy, disappeared and was replaced by an invasion of the offshore population. (For a more detailed account of seasonal changes in the neritic community see p. 300.)

The annual cycle of the neritic community in boreal waters in 1931-1932 contrasts in an interesting manner with that of the region immediately south of cape Cod. In the vicinity of Woods Hole neritic species occur throughout the year, being divided roughly into two groups—a summer community and a winter community (Fish 1925, p. 141). In early summer *Acartia tonsa* usually dominates. Later *Pseudodiaptomus coronatus* appears, reaches its peak in late fall and remains well into the cold months. The winter community is composed of a much larger number of neritic species, *Acartia clausi, A. longiremis, A. bifilosa, Eurytemora herdmani, E. hirundoides,* and *Centropages hamatus. Tortanus discaudatus*

appears during the late winter, reaches its maximum in February and March, and declines with the warming of the water. Considering this seasonal variation it will be seen that the summer and autumn forms are southern ranging species (Wilson 1932b) not reported from the gulf of Maine, and the winter and spring forms are boreal species which in 1931 and 1932 comprised the summer neritic community in the gulf.

Reflecting to a large extent conditions in inland waters, considerable annual variation may be expected in the neritic stock occurring in the open gulf and bay. The extent of this variation cannot be clearly determined on the basis of available records. Certainly there is no distinctly winter neritic community corresponding to that occurring south of the cape, although a wide range in the seasonal occurrence of some of the neritic species which formed the summer population in 1931-1932 has been reported by previous observers. In the case of *Acartia clausi,* one

TABLE IX. Neritic zooplankton species. Relative

Area	Total region					Western area		
Month 1932	Apr.	May	June	Aug.	Sept.	Apr.	May	June
Cruise	26	27	28	30	32	26	27	28
Acartia clausi				.01				
Acartia longiremis			.1	.2	.8			T
Centropages hamatus				T				
Eurytemora herdmani				T	T			
Tortanus discaudatus	.01	.01	T	T	.01		T	T
Evadne nordmanni	T	.06	.1	2.1	T	T	.2	.4
Podon leuckarti			.1	T				.6
Bougainvillia superciliaris		T	T	T				
Halopsis ocellata		T	.05	T			T	T
Hybocodon prolifera	.01	.1	.02			T		
Melicertum campanula				T				
Mitrocoma cruciata		T	.03				T	T
Obelia sp.		T	T	T	T			T
Phialidium languidum	T		T	4.4	1.1			T
Sarsia sp.		T	T	T	T			
Staurophora mertensii		T	T	T				T
Syncoryne mirabilis		T						
Turris vesicaria				T	T			
Aurelia aurita	.07	T	T					
Cyanea capillata var. arctica		T	T	T				T

of the most important neritic species, its presence in the gulf in the summer of 1912 and 1915, and apparent absence during the winter of 1912-13 would accord with more recent observations. On other occasions it has been taken in the spring (1915, 1920) and winter (1920-31) (Bigelow 1926, pp. 172-174). Willey (1921, p. 187) also found it forming 68 per cent of the copepod population of Passamaquoddy bay on January 16, 1920. On the basis of these records Bigelow suggested two breeding seasons for *A. clausi* in the gulf, one in early spring and the other in late summer. It may be suggested that the late summer season may prove to be more general and represent the local stock, and that in some years winter breeding, centred south of cape Cod, may extend east into the gulf to form an early spring crop. This is indicated by the absence of spring records from the bay of Fundy and the fact that the largest numbers in April 1915 were recorded

in the outer banks (Georges and Browns) and off cape Cod (Bigelow 1926, p. 175). Considerable seasonal variation is also indicated in previous records for other species of neritic copepods, but with the exception of *A. clausi* all show a definite maximum in summer and early autumn and a minimum in winter and early spring. Earlier records of Cladocera are all limited to the period between June and September (Bigelow 1926, p. 307) and Medusae between April and October.

Evaluation of species. The quantitative variation of neritic species was even more marked than their restricted geographical range. The local irregularities commonly encountered offshore would quite naturally be expected in regions where the neritic populations of neighbouring bays are frequently dominated by different species (p. 288). Qualitatively each bay must be considered as an independent unit, but for the inner gulf and bay of Fundy outside of the headlands,

percentages in metre net collections in 1932.

Central area							Bay of Fundy				
Aug.	Sept.	Apr.	May	June	Aug.	Sept.	Apr.	May	June	Aug.	Sept.
30	32	26	27	28	30	32	26	27	28	30	32
										.05	
T				.1	.2				.3	.5	2.5
										.01	
										.01	T
T		.04						.03	T	.01	.04
.6			.03		2.3			.01	.03	2.7	T
				T						T	
T								T	T	T	
T			T	.04				T	.1	T	
							.04	.4	.06		
T					T					T	
			T	T				T	.1		
T			T	T				T		T	T
.7	T	T			.6				T	8.4	3.4
T	T		T	.02	T			.02			
				T				T	T	T	
			T								
T					T					T	T
							.2	T	T		
			T					T	T	T	

values obtained by averaging all stations in each of the general areas are considered reasonably representative, at least for the more abundant species.

Of the two common species of Scyphomedusae, swarms of *Aurelia aurita* were frequently encountered in bays, but with one exception, at station 10 in the bay of Fundy, on September 4, 1931, never offshore in quantities sufficient to interfere with the normal fishing of the nets. Whenever taken this species was observed at or near the surface during the interval of towing, and the numbers in the hauls would indicate that it was concentrated largely in the upper levels and captured in representative numbers. *Cyanea capillata var. arctica* appeared in oblique hauls but was less frequently seen at the surface. Again the frequency with which the long tentacles were found on the cable and net bridle when none appeared in haul suggests that this species is widespread near the coast in deeper

water. When one considers the length of the expanded tentacles of *Cyanea,* it is not surprising that less than 10 per cent of those coming in contact with the lines entered the nets, and there is no reason to suppose that the collection records are any less representative than in the case of *Aurelia.*

Bay of Fundy. As previously stated, but one neritic form, *Acartia longiremis,* was taken between October 1931 and April 1932, and this reached its peak in September. Its occurrence during the year was as follows: 1931, July 0.1 per cent, August 0.05 per cent, September 0.02 per cent, November T, December 0.04 per cent; 1932, January 0.7 per cent, March 0.3 per cent, June 0.3 per cent, August 0.5 per cent, September 2.5 per cent. The values for other species during the period, April to September, are shown in table IX. Until mid-summer the total of all neritic species did not exceed 0.6 per cent at any time. *Phialidium* then increased to 8.4 per cent of the population, and *Evadne,* 2.7 per cent in August. The former species remained abundant (3.4 per cent) and with *Acartia longiremis* (2.5 per cent) dominated the neritic stock in the bay in September.

Comparing the mean values for the period, July-August in 1931 (shown below) and 1932 (table IX), the most striking difference occurred in *Acartia clausi,* which appeared much later in the second year (p. 294), and, although abundant in Passamaquoddy bay in late summer, had not become very widely distributed in the bay of Fundy by September.

	Per cent		Per cent
Acartia clausi	4.0	*Obelia sp.*	0.07
Acartia longiremis	0.06	*Phialidium languidum*	1.3
Tortanus discaudatus	0.07	*Podocoryne carnea*	T
Evadne nordmanni	0.07	*Tiaropsis diademata*	T
Podon leuckarti	T	*Turris vesicaria*	T
Podon polyphemoides	T	*Aurelia aurita*	T

Phialidium in both years formed an important member of the neritic population of the bay, a population totalling 19 species. Of these, 16 species were found in 1932 and 12 in 1931. Seven of the species taken in 1932 did not appear in the collections from the bay in the first year, and two species occurred only in 1931.

Inner gulf. In the inner gulf during the summer of 1932, 15 neritic species were taken in the western area and 13 in the central area (table IX). Of these, three, *Bougainvillia, Hybocodon,* and *Obelia,* found in the western area, did not appear in the central area, and one, *Syncoryne,* occurred only in the latter. Because of the small numbers involved these distribution records are not significant, and it is probable that all species range throughout the region, as indicated by the fact that all reported from the western area in 1932 were also found in the bay of Fundy.

The values in the gulf were at all times almost negligible, never exceeding 1.3 per cent in the western area even at the peak of the season (August). In the central area the actual numbers were still less, but due to a smaller representation of offshore species, the percentages of neritic forms were at times somewhat higher, reaching 3.1 per cent in August when *Evadne nordmanni* dominated.

Outer gulf. Both in the eastern and western Atlantic neritic species have been reported on offshore banks, the populations frequently corresponding to some extent with those at similar depths in the neighbouring coastal zones. On the Grand banks in early June 1924 the senior author found the following neritic species together with larvae of numerous benthonic species: *Centropages hamatus, Cyanea capillata, Lizzia grata, Sarsia flammea, S. mirabilis, Tiaropsis diademata,* and *Turris vesicaria.*

In the gulf of Maine Bigelow (1926) reported *Acartia clausi* at times numerous in the vicinity of the outer banks (p. 174), *A. longiremis* particularly in the region of Georges and Brown banks (p. 177), and *Tortanus discaudatus* on German bank (p. 294). In 1927 *Acartia clausi* and *Centropages hamatus* were taken on Georges bank in early August. Medusae have also been reported frequently from this region by Bigelow.

There are unfortunately no data from the offshore banks at the peak of the season (August) in 1931-32, but observations in April and September of the second year indicate that the numbers of neritic forms were everywhere very sparse in the outer gulf. In May stations in the eastern channel, Browns bank, and the central basin of the gulf yielded no neritic species, but in the western basin one species, *Evadne nordmanni* averaged 0.2 per cent. In September negative results were obtained on Georges bank, off the west coast of Nova Scotia, and the central area of the gulf, but a few specimens of *Turris vesicaria* were found along the inner margin of Georges bank. It would thus appear that neritic species may be expected in the region of offshore banks, particularly during the propagation seasons, but they are evidently more irregular and remain for shorter periods than in the coastal zone. They are rarely very widespread offshore at any time.

As the area covered in the gulf in 1931 extended well inside of the 100 metre contour (fig. 1), the results are not comparable quantitatively with those of 1932. They are, however, indicative of a marked increase of neritic forms upon approaching the coast, as mentioned on p. 253, although the number of different species was less in both the western and central areas than in 1932. Had observations extended throughout the summer in 1931 the number of Medusae at least would certainly have been greater.

Two species, *Podon polyphemoides* and *Podocoryne carnea,* widespread in both the gulf and bay in 1931, were not found the following year, even in bays visited in August and September. A third species, *Steenstrupia virgulata,* found only in the western area during the first season, was also not taken again. Comparing table IX with the following records for August 1931 in the gulf, it will be seen that seven species were added in 1932:

	Western area (per cent)	*Central area* (per cent)
Acartia clausi	2.0	3.3
Acartia longiremis	1.9	5.0
Centropages hamatus		.02
Eurytemora herdmani	.8	.02

	Western area (per cent)	*Central area* (per cent)
Tortanus discaudatus	2.1	.14
Evadne nordmanni	6.8	3.1
Podon leuckarti	4.2	T
Podon polyphemoides	7.2	3.3
Melicertum campanula		T
Obelia sp.	.6	.1
Phialidium languidum	1.3	.6
Podocoryne carnea	T	T
Steenstrupia virgulata	.07	

FISH EGGS AND LARVAE

Almost all teleosts in the gulf of Maine have pelagic young, and in a relatively large percentage the eggs are buoyant. With few exceptions, they are endemic boreal species. Exceptional are the larvae of *Zoarces anguillaris* (viviparous) and *Opsanus tau* (demersal eggs) which apparently remain at or so near the bottom that they are not taken in plankton collections.

Number of species. Within the gulf, Bigelow and Welsh's records (1925) indicate that approximately 54 species probably breed to some extent, and the larvae of at least 41 may be expected in the open waters north of cape Ann. Neritic minnows and summer migrants, with the exception of *Scomber scombrus* and possibly *Poronotus triacanthus,* would be excluded. Prior to 1931 pelagic eggs of about 15 and larvae of some 31 species had been identified in tow net collections from the gulf and bay of Fundy. Immigrant elvers of *Anguilla rostrata* had also been regularly taken between February and April (Bigelow and Welsh 1925).

The present collections, not covering the winter months in the gulf, have yielded young of 28 species and distinguishable eggs of 10 species. Probably some *Melanogrammus* eggs were taken in April and May, and *Merluccius* during the summer, but as none were in advanced stages, the former were indistinguishable from those of *Gadus* and the latter from *Enchelyopus. Merluccius* eggs in late embryonic stages, and larvae were found in some of the bays, particularly in the western area in August, 1929 and 1932 (see table XIX).

The larvae and fry represented 24 detectable endemic species, one questionable form, *Siphostoma fuscum* (possibly endemic) from Georges bank, and three not identified. Eggs and young taken during the period from July 1931 to September 1932 are listed below.

Ammodytes americanus (larva)
Anarhichas lupus (larva)
Anguilla rostrata (elver)
Argentina silus (fry)
Aspidophoroides monopterygius (fry)
Brosmius brosme (egg and larva)
Clupea harengus (larva and fry)

Cyclopterus lumpus (fry)
Enchelyopus cimbrius (egg and larva)
Gadus callarias (egg, larva and fry)
Glyptocephalus cynoglossus (egg and larva)
Hippoglossoides platessoides (egg and larva)
Leptocephalus conger (larva)
Limanda ferruginea (egg)
Lophopsetta maculata (larva)
Lumpenus lampetraeformis (larva)
Melanogrammus aeglifinis (larva and fry)
Merluccius bilinearis (larva)
Myoxocephalus scorpius (larva)
Neoliparis altanticus (larva)
Pholis gunnellus (larva)
Pollachius virens (larva)
Sebastes marinus (larva)
Siphostoma fuscum (fry)
Tautogolabrus adspersus (egg and larva)
Urophycis chuss (egg)
Scomber scombrus (egg)

Comparing the gulf with adjoining regions, immediately south of cape Cod, Edwards obtained 34 species of larval fishes at Woods Hole over a period of fifteen years, and the senior author 21 species in 1922-1923 (Fish 1925). There, however, the composition of the population is different, and at least 50 per cent of the larvae taken were migratory southern ranging species which enter the region and breed during the summer. East of the gulf, Dannevig (1919, p. 5) lists 36 species of eggs and larvae obtained in Canadian waters between May and August in 1915, of which only about 15 were taken off the eastern Nova Scotian coast. The latter area he found populated by definitely boreal species as contrasted with boreo-arctic forms encountered upon approaching Newfoundland.

Seasonal variation. Unlike the pelagic invertebrate population of the gulf in which there was no evidence of appreciable breeding between October and March, with the exception of *Pleurobrachia pileus* (p. 300), fish eggs and larvae were found throughout the year. Of the 54 species mentioned on p. 258, 31 spawn between May and September, 9 between February and April, and 14 in late autumn and winter.

Winter spawners include most of the sculpins, some of the blennies (*Pholis, Lumpenus*), gadoids (*Pollachius, Microgadus, Urophycis tenuis*), flounders (*Paralichthys dentatus, Pseudopleuronectes dignabilis*), and a few others like *Liparis, Cryptocanthodes* and *Anarhichas.*

The number of summer breeders is enlarged by small forms frequenting inland waters such as *Fundulus, Menidia, Pungitius, Gasterosteus,* and *Apeltes,* and southern ranging species restricted largely to Massachusetts bay during the warm months, *Cynoscion, Tautoga,* and *Paralichthys oblonga* (*Roccus, Steno-*

tomus, and *Spheroides,* brackish water spawners, enter the region, but probably never breed there). Omitting these two groups there remain approximately 18 known endemic species whose early larvae can be expected offshore in the gulf during the summer, a number not very much larger than the winter group.

The spring group appearing during the period of greatest zooplankton augmentation, comprises some of the most numerous fishes in the region, *Clupea, Gadus, Melanogrammus, Pseudopleuronectes americanus, Ammodytes, Cyclopterus,* and *Myoxocephalus aeneus.* At least one spring spawner, *Gadus,* continues breeding well into the summer in the eastern gulf.

The breeding season of at least one species, *Zoarces anguillaris,* may be restricted to late autumn. Another, *Clupea harengus,* spawns in both spring and autumn in some localities in the eastern portion of the region, but only during a

TABLE X. Total numbers of young fishes taken during the

Locality	Western area				
Number of stations	7	7	7	7	2
1932	Apr.	May	June	Aug.	Sept.
Ammodytes americanus	3	1			
Anguilla rostrata (elver)	1				
Argentina silus					
Asidophoroides monopterygius					
Brosmius brosme				9	
Clupea harengus					
Enchelyopus cimbrius			2		
Gadus callarias (larva)					
Gadus callarias (fry)			4		
Glyptocephalus cynoglossus				7	
Hippoglossoides platessoides			12	1	
Leptocephalus conger (leptocephalus)					
Lumpenus lampetraeformis				3	
Melanogrammus aeglifinus			7		
Merluccius bilinearis					
Myoxocephalus octodecimspinosus					
Myoxocephalus scorpius					
Neoliparis atlanticus					
Pholis gunnellus					
Pollachius virens (fry)					
Sebastes marinus			1331	1565	

relatively short period in late summer or autumn in the western gulf, the season tending to be progressively later to the westward (Bigelow and Welsh 1925, p. 25). South of cape Cod, at Woods Hole, no larval *Clupea* were taken in 1922 or 1923, but Edwards found them in varying abundance each year from 1893 to 1907 (Fish 1925, fig. 76). Although appearing in every month except August at sometime during this period, in 10 of the 15 years there were very definite spring and autumn groups, occurring most commonly in April-May and November-December.

1931 and 1932. Eggs taken during the winter months in the bay of Fundy proved particularly troublesome because they were almost invariably in early stages and could not be identified with certainty. It would appear that in 1931-32 cod (1.4-1.45 mm.) may have continued spawning through October, and pollock (1.15-1.2 mm.) from November to January (February records destroyed) in New

Brunswick waters. On the Nova Scotian side of the bay what are assumed to have been cod (1.42-1.7 mm.) had begun to spawn as early as January 6. No cod or pollock larvae were taken during this time and with the exception of two specimens of *Clupea harengus,* one (24 mm.) at sta. 5 on November 11, and another (21 mm.) at sta. 6 on November 12, no larvae appeared after September 1931 until the following April. Occasional specimens of *Clupea* in advanced stages were also taken by the Nova IV in Nova Scotian waters in December and January. On March 5 three eggs of *Hippoglossoides* appeared in the Quoddy region (sta. 5) with five others which may have been either cod or haddock.

The seasonal distribution of eggs and larvae in the bay between April and September (1932) is shown in table XIII. It will be seen that eggs or young of 10 species appeared in April, and until late September no less than five were found

period, April-September, 1932. Larvae unless otherwise indicated

Central area					Bay of Fundy				
8	7	7	8	1	12	12	12	12	11
Apr.	May	June	Aug.	Sept.	Apr.	May	June	Aug.	Sept.
1					2				
1					2				
			1					1	
						2	5		
			10				1	1	
1			1	5	3			629	2683
		1						1	
	4						1		
			16				5	9	3
							10		
			1						
	2	1				5	1	2	
		23	6	4			91	4	
			1						
					1				
2	3				1	8	1		
							11		
	2				1	50	5		
					1				
	11	343	971	1		1	5	50	1

at any time. The largest variety occurred in June and August. Of the forms taken in the inner gulf in 1932 only two larvae, *Leptocephalus conger* and *Merluccius bilinearis* were absent in the collections from the bay.

In 1931 six species were taken in August and September, eggs of *Enchelyopus, Glyptocephalus, Tautogolabrus* and *Merluccius,* and larvae of *Sebastes* and *Clupea.* Monthly collections at one station in the bay over a period of ten months in 1917 yielded eggs of but one species, *Hippoglossoides,* which formed 1.5 per cent of the zooplankton population on April 1, and no larvae.

The seasonal occurrence of eggs and larvae in the inner gulf in the summer of 1932 conforms with previous observations (table XIII). Several species showed a prolongation of the spawning season to the eastward. This was not evident in *Hippoglossoides* whose eggs occurred at the same time (April-May) throughout

the region, but *Gadus-Melanogrammus* eggs, which had largely disappeared in the western area by the end of May, were equally abundant east of Mount Desert in June, and in the bay reached their peak in the latter month. Larvae of several species such as *Pholis, Myoxocephalus, Lumpenus, Glyptocephalus* and *Gadus* were present in the Fundy region a month after they had disappeared in the gulf (table X).

FIGURE 26 (part)

The occurrence of 12 species in the gulf in August 1931 is shown in table XIV. Representing conditions nearer the coast, both eggs and larvae of *Enchelyopus* were very much more abundant and there were larvae of three species, *Cyclopterus, Lophopsetta,* and *Tautogolabrus,* not found at all at the more offshore stations of the next year. Single specimens of *Lophopsetta* and *Tautogolabrus* were taken on Georges bank in September 1932.

Regional variation. The geographical distribution of eggs and larvae in the gulf has been so fully described by Bigelow and Welsh (1925) that little need be added here except to contribute data for 1931-32. Considering the size of the adult stocks of some species, it might appear that the numbers in our collections are surprisingly small. However, previous observers have experienced similar results, particularly in the case of larvae. Eggs have on occasions been taken in

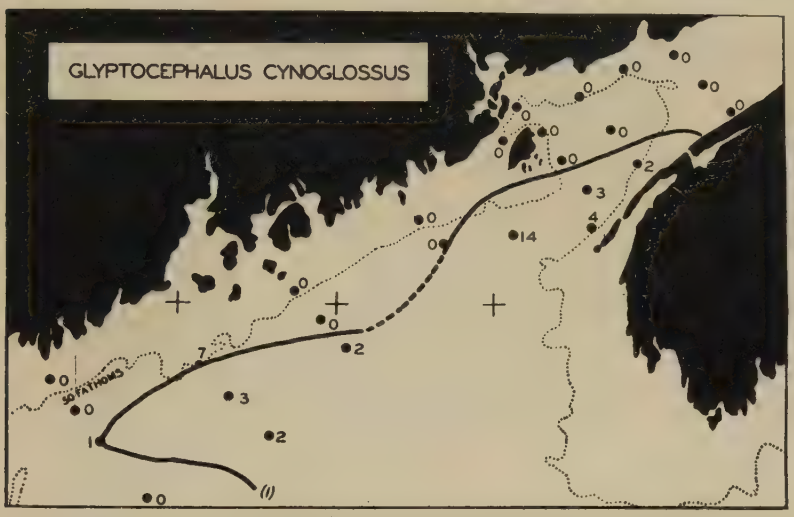

FIGURE 26 (con.). Distribution of larvae of representative species having demersal (upper) and pelagic (lower and right) eggs. Number of individuals per haul.

abundance. In Massachusetts bay in April 1924, 8,148 *Gadus-Melanogrammus* eggs were obtained in a 20 minute foot-net haul, with an average for 20 stations (metre net) of 1038 eggs (Fish 1928, pp. 260 and 268). It seems probable that such rich hauls are to be expected only in the immediate vicinity of limited spawning areas (Bigelow 1926, p. 49). Dispersal of later stages and a consequent reduction in the number per unit of area would inevitably result in the case of species in which the adults occur largely in local concentrations. It is also possible that in the eastern part of the gulf where breeding of such forms as the cod extends over a relatively long period, spawning is never as intense as in the region west of cape Elizabeth. Larvae of two species, *Clupea* and *Sebastes,* one having demersal eggs and the other viviparous, were at times abundant, but our observations did not extend sufficiently far west to include the area where larvae of species having buoyant eggs have been reported most numerous (Bigelow and Welsh 1925, p. 309).

The winter observations in the bay of Fundy, described on p. 260, indicate that pollock were spawning in the New Brunswick waters in November and December, and in early January cod began breeding, first along the Nova Scotian coast. From the distribution during this period it would appear that propagation took place along the two sides of the bay but the eggs did not survive long enough to become

very widely dispersed. This is suggested both by their absence at the offshore stations and the extreme scarcity of advanced stages in all collections in the bay from November to the end of January, a condition according with Huntsman's theory that in the bay of Fundy propagation of most, if not all, species having pelagic eggs is largely unsuccessful (1918, p. 65). In figure 26 it will be seen that at their periods of maximum abundance in the Fundy region in 1932, the young

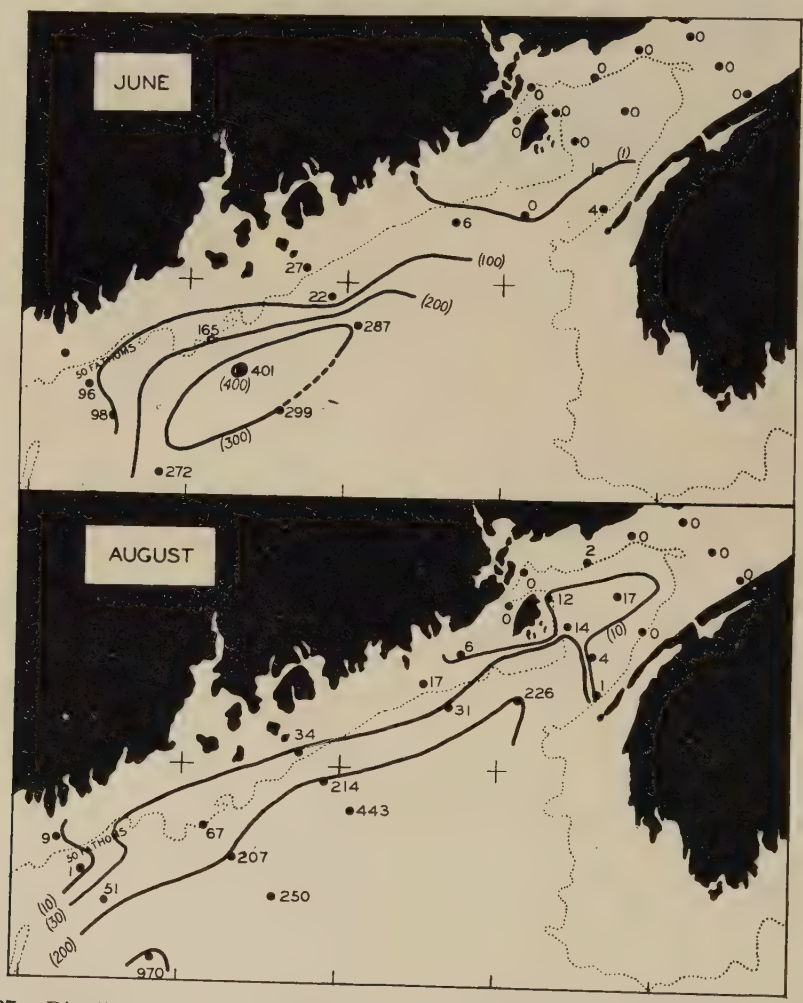

FIGURE 27. Distribution of *Sebastes marinus* larvae in June and August, 1932. Number of individuals per haul.

of *Pholis* (demersal eggs) were concentrated in the inner bay, but there was little evidence of successful local propagation of *Melanogrammus* and *Glyptocephalus* (buoyant eggs) or survival of larvae entering from outside waters.

The regional distribution in the inner gulf and bay during the summer months is shown in tables X and XIII. Of the two most abundant species in the collec-

tions, *Sebastes* and *Clupea,* the former propagates indifferently in both deep and shallow water (Bigelow and Welsh 1925, p. 309) and has been included by Huntsman (1922, p. 16) in the group breeding successfully in the Fundy region. Appearing first in the eastern gulf in May in 1932, larval *Sebastes* soon became widely distributed, but as shown in figure 27, were everywhere found in the greatest abundance at the outermost and deepest stations, particularly in the western area. In the bay only one specimen was taken in 1931 (sta. 10 September), and in 1932, although somewhat more numerous particularly in August, the numbers were relatively small and restricted largely to the deeper water in the central basin (fig. 27). It is quite possible that these may have entered from the gulf, although their absence along the Nova Scotian side, where immigrants are usually most numerous, may be indicative of local propagation.

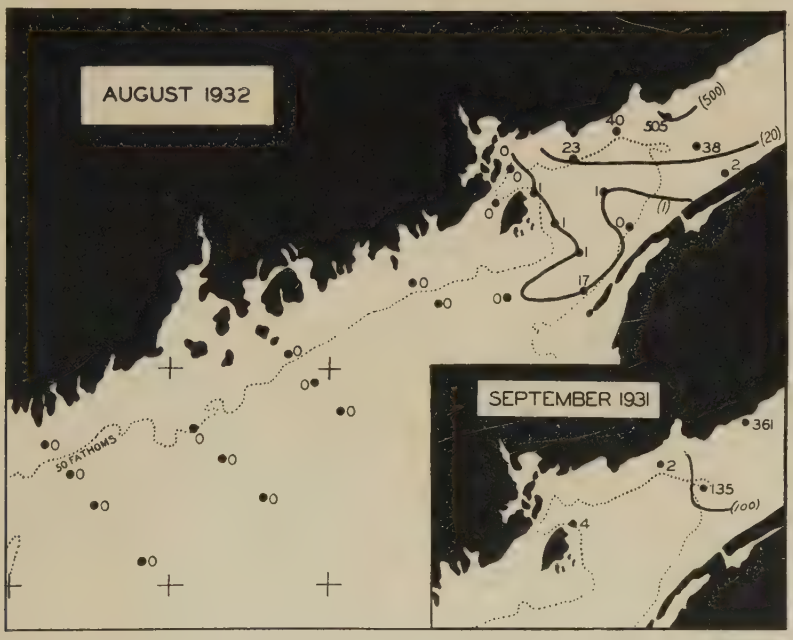

FIGURE 28. Distribution of *Clupea harengus* larvae. Number of individuals per haul.

Clupea harengus spawns in the gulf in summer and autumn, but in the Fundy region, at least in Nova Scotian waters, both spring and autumn spawning takes place (Bigelow and Welsh 1925, p. 95). Centred largely offshore, collections have yielded very few larvae in the gulf during the spawning season. In Gloucester harbour, however, Bigelow and Welsh (1925, p. 100) found a swarm of early larvae from 9 to 11 mm. in late October, and occasional advanced stages (26 to 50 mm.) widespread in the gulf in March and April. Two specimens, 33 mm. in length, were taken in the spring of 1932, both appearing off Mount Desert (sta. 32) on April 22. None were found as far west as this point in the summer or autumn of either year. In the central area in 1931 one individual (9 mm.) was taken at sta. 34 on August 15, and in 1932 five specimens (12-13 mm.) at sta. A1409.

In the bay of Fundy occasional specimens were found in April, but our collections showed little if any evidence of a spring crop. Graham (1936, p. 111) also found that . . . "spring spawning produces no considerable contribution to the herring stock." In New Brunswick waters (sta. 11A and 12) two measuring 43 and 45 mm. appeared on April 18-19 in 1932. On the Nova Scotian side at this time a single individual, 30 mm. in length, was taken at sta. 9 and in zooplankton samples contributed by Mr. Graham from the upper bay (sta. N173, N174, N176) there were six specimens ranging from 23 to 26 mm. (Some larvae may have been removed from the Nova IV samples.) The fact that Bigelow and Welsh (1925, p. 95) found in the gulf members of the autumn stock as small as 26 mm. in April,

TABLE XI. *Clupea harengus.* Length frequency of young in plankton collections, August and September, 1932

1932	Station	Date	Length in mm.			
			7.5-11	12-14	15-19	20-30
August.....	6	18	1			
	7	17	1			
	8A	17	17			
	9	19	2			
	10A	19	38			
	11A	19	502	3		
	12	20	39	1		
	13	21	23	1		
	34	15	1			
	36	18		1		
September.....	7	14			2	
	8A	14	1,651			
	9	16	13		9	2
	10A	16		13	7	
	11A	16	1	1		
	12	16		4		
	13	16	47	34	45	23
	36	15	1		6	
	37	15	818	2	1	3

indicates that our specimens were probably of a similar age. These must have left the surface waters soon after this time because none were taken in metre net hauls during May, June or July.

The distribution of larvae in August and September would indicate two distinct sources of the summer-autumn crop, one centred in the inner bay, probably in New Brunswick waters, and the other on the Nova Scotian coast near or outside of the entrance. In 1932, what for purposes of distinction will be called the New Brunswick stock, was found first in mid-August. At this time (fig. 28) propagation appeared to be centred near the coast east of Saint John, where 505 larvae were taken at sta. 11A. As shown in the following table all of these were

very small, rarely exceeding 12 mm. None were found in the outer Quoddy region and very few on the south side of the bay. This crop diminished rapidly and although widespread in the bay in mid-September, their numbers were very sparse (table XI), except at sta. 13 off Pt. Lepreau where 68 specimens, exceeding 15 mm., were taken. It is surprising that so few of this size were found in the outer part of the bay (none in the Quoddy region) and along the adjoining

TABLE XII. *Clupea harengus*. Length frequency of young in plankton collections in 1931

1931	Station	Date	Length in mm.			
			7.5-11	12-14	15-19	20-30
August.....	14	18	3			
September.....	6	6			4	
	10	4		129	4	2
	11	4	355		5	1
	12	1	2			
	5	29			2	
	6	30		1	5	
	8A	30			2	
November.....	5	11				1
	6	12				1

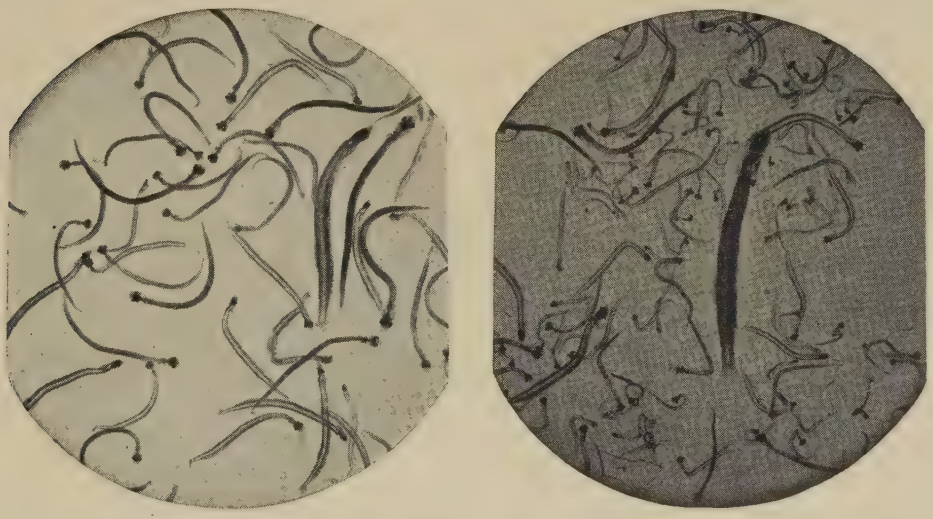

FIGURE 29. *Clupea harengus* taken at stations 10 (left) and 11 (right) on September 4, 1931. Same magnification.

coast of Maine where they would have been expected to drift in a month's time. Indication of the second source of supply became evident in mid-September with an apparent influx of early larvae from outer Nova Scotian waters, 1,651 specimens being taken at sta. 8A (fig. 30). Their small size and absence in collections from the eastern gulf, suggest relatively local origin. Occasional large specimens, 22

to 30 mm., also appeared at this time but their source is uncertain. If they represented the local spring crop it is strange that none were taken in the collections of May, June, July and August.

In 1931 the rather fragmentary records indicate that active spawning of the New Brunswick stock apparently took place somewhat later, and that of the Nova Scotian stock somewhat earlier than in the following year. On September 4, 361 specimens were taken at sta. 11 (13 miles east of cape Spencer), but larvae had not become very greatly distributed westward in New Brunswick waters because just two were found off Saint John (sta. 12) on September 1 and four at sta. 6 on September 6 (fig. 28). Also on September 4 a different size group, comprising

TABLE XIII. Occurrence of fish eggs and young in

	Total region					Western area		
	Apr.	May	June	Aug.	Sept.	Apr.	May	June
Ammodytes americanus larva	T	T				T	T	
Anguilla rostrata elver	T					T		
Argentina silus larva				T				
Asidophoroides monopterygius		T	T					
Brosmius brosme egg			T	T				T
Brosmius brosme larva			.03	T				.1
Clupea harengus larva	T			T	.2			
Enchelyopus cimbrius larva			T	T				T
Enchelyopus cimbrius egg		.04	T		T			T
Enchelyopus-Merluccius egg			.3	.4	.03			.9
Enchelyopus-Merluccius-Urophycis egg			T	.3				T
Gadus callarias egg	T	T						
Gadus callarias larvae		T						
Gadus-Melanogrammus egg	.3	.5	.4			.2	T	T
Gadus-Glyptocephalus egg			T	.04				
Glyptocephalus cynoglossus larva			T	T	T			
Hippoglossoides platessoides egg	.2	.1	T			.1	.03	T
Hippoglossoides platessoides larva			T					
Leptocephalus conger, leptocephalus				T				
Limanda ferruginea egg			T	T				T
Lumpenus lampetraeformis larva		T	T	T				
Merluccius bilinearis larva				T				
Myoxocephalus octodecimspinosus larva	T							
Myoxocephalus scorpius	T	T						
Neoliparis atlanticus larva			T					
Pholis gunnellus larva	T	.01	T					
Pollachius virens larva	T							
Sebastes marinus larva		T	.1	.2	T			.3
Melanogrammus aeglifinus larva			T	T	T			T
Gadus callarias, fry (20-25mm.)			T					T
Urophycis chuss egg		T		T				
Scomber scombrus				T				

135 specimens and believed to represent the Nova Scotian crop, were found in the mid-bay (sta. 10) along the course of the drift from outside waters. Whereas 355 of the 361 larvae at sta. 11 were 7 to 12 mm. in length, all of those at sta. 10 ranged from 11 to 19 mm. with the exception of two having a length of 23 mm. The difference in the average size of the larvae in the two groups can easily be seen in figure 29. Further evidence of different origin is indicated by the volume and character of the zooplankton communities in the two localities. At sta. 10 in the path of the entering drift, with a volume of 470 cc., the population was typical of the open bay. *Calanus finmarchicus* and *Centropages typicus* formed 89.4 per cent and other typical open gulf species like *Pseudocalanus, Sagitta,*

Metridia, Tomopteris, Meganyctiphanes eggs, and *Limacina* were present in smaller numbers. At sta. 11 the volume amounted to only 15.5 cc. and, although *Calanus* and *Centropages* formed 45.1 per cent, the remainder of the community was typically neritic containing such species as *Littorina* larvae 6.6 per cent, macruran larvae 6 per cent, *Cancer* zoea 5 per cent, *Crago* larvae 1.8 per cent, *Balanus* nauplii 2 per cent, *Hyas* zoea 0.6 per cent, and several other forms equally characteristic of shallow water.

Evaluation of species. Like adult euphausiids, larval fishes, because of their size, were at times prominent, but numerically they never formed an appreciable factor in the collections except at the above mentioned station in the bay (sta.

1932. Relative percentages in metre net collections

Central area							Bay of Fundy				
Aug.	Sept.	Apr.	May	June	Aug.	Sept.	Apr.	May	June	Aug.	Sept.
		T					T				
					T		T			T	
T					T			T	T		
T					T				T	T	
		T			T	T	T			T	.5
				T						T	
			.03	T				.1			T
.3				T	.7				T	.1	.1
.6				T	.2				T	.05	
			T				.01	T			
			T						T		
		.5	.6	.1			.3	.8	1.2		
					.03				T	.1	
T					T				T	T	T
		.4	.1				.1	.2			
					T				T		
					T						
T										T	
T			T	T				T	T	T	
					T						
							T				
		T					T	T	T		
							T		T		
			T				T	.03	T		
							T				
.3			T	.1	.2	T		T	T	T	T
				T	T	T			T	T	
T											
T					T						

11) where larval *Clupea* comprised 10.1 per cent of the scanty haul in September 1931. Relative values during the period of greatest abundance in 1932 are shown in table XIII. To this list may be added one specimen of *Anarhichas* (24 mm.) taken by the Nova IV near sta. 10A and several *Cyclopterus* dipped from floating weed in the bay in June. Collections from the outer gulf and Georges bank in September yielded three *Argentina* (33-41 mm. sta. A1411 and A1412), one *Glyptocephalus* (40 mm., sta. A1411), one *Lophopsetta* (4 mm., sta. A1416), one *Tautogolabrus* (14 mm., sta. A1414) and two *Siphostoma* (40 mm., sta. A1414 and 48 mm., sta. A1416).

The following values were obtained in August and September 1931:

TABLE XIV. Occurrence of fish eggs and young in 1931. Relative percentages in metre net collections

Area	Western	Central	Bay of Fundy	
Month	August	August	August	September
Brosmius brosme egg		0.15		
Clupea harengus larva			T	0.8
Cyclopterus lumpus fry	T	T		
Enchelyopus cimbrius egg	5.4	1.2	0.2	T
Enchelyopus larva	T	0.04		
Enchelyopus-Merluccius egg				0.6
Gadus callarias egg	T			
Gadus-Glyptocephalus egg	0.2	0.8	T	0.01
Glyptocephalus cynoglossus egg	T	T		
Glyptocephalus cynoglossus larva	T			
Lophopsetta maculata larva	T			
Lumpenus lampetraeformis larva	T	T		
Neoliparis atlanticus larva	T	T		
Sebastes marinus larva		T		T
Tautogolabrus adspersus egg	0.1	0.2		0.05
Tautogolabrus adspersus larva	T	T		
Urophycis chuss egg	T	T		
Egg, sp. (1.75-1.85 mm. oil glob. 6 n m.	T	T		

It will be noted that with the exception of *Clupea* and *Sebastes* no larvae were found in the bay of Fundy at this time.

LARVAE OF BENTHONIC INVERTEBRATES

To one familiar with the benthonic fauna south of cape Cod, that of the gulf of Maine contrasts strikingly in two respects, the apparent duration of the breeding seasons, and the relatively few species represented in the collections.

There is a wide variation in the length of the spawning periods exhibited in different species in both regions, but considering the fauna as a whole certain general characteristics are noticeable. Species whose normal range does not extend north of the cape tend to have a very short breeding period, sometimes less than a week, and the pelagic larvae are not commonly taken for more than a month or two at the most. Some of the boreal forms in the gulf of Maine such as *Asterias, Lepidonotus, Crago,* certain of the nereids and members of the genus *Spirontocaris* appeared in offshore collections for only a short time, usually in April or May (table XV), but records from inland waters (table XVIII) showed most of these species still spawning actively in mid-August. It would therefore appear that except at the height of the season many of these species are not present in sufficient numbers beyond the confines of bays to be sampled regularly. Larvae like *Eupagurus, Cancer,* and *Hyas,* occurring in larger numbers outside of the headlands were taken from April to September, particularly in the eastern gulf. In the bay of Fundy the season in some cases may be even longer. There zoea

of *Cancer* occurred from April to December, one species of *Spirontocaris* from July to November, and *Littorina litorea* from April to September.

In species endemic over a wide area, the breeding period may be either equally long throughout the range or somewhat reduced south of cape Cod. Thus *Crago* larvae occur at Woods Hole from May to mid-December and *Eupagurus* from April to November, but *Cancer* zoea appearing in mid-May are rarely found after early August, and *Littorina* larvae only from March until July (Fish 1925, p. 136). Even the more reduced breeding seasons of boreal species south of the cape are relatively long compared with most of the southern ranging species, as indicated in the records for 1922-1923 (Fish 1925, figs. 56 and 59).

FIGURE 30. Distribution of *Clupea harengus* larvae in September, 1932. Number of individuals per haul.

In some benthonic species, like certain pelagic invertebrates and teleosts, spawning begins first in the western portion of their range and is progressively later to the eastward. Here again, however, there is a wide variation, some showing little or no difference and a few starting considerably earlier in the eastern gulf. *Balanus balanoides* shows a definite delay to the eastward. At Woods Hole nauplii are liberated in early December although they may be found within the shells of the adults several months earlier. In Massachusetts bay Bigelow took nauplii in March and early April, but after April 12 only "cyprids" were found

(1914a, p. 408). Farther east in 1932 small number of nauplii were taken in metre net collections as far west as Casco bay in late April, but as shown in figure 31, the oblique hauls with a smaller net of finer mesh indicate production centred at this time in the outer part of the bay of Fundy and along the west coast of Nova Scotia, with some spawning on Georges bank. The season was evidently almost over west of Mount Desert although small numbers of nauplii were found at 86 per cent of the stations in the western area. In the central and Nova Scotian areas they were taken at all stations, being particularly abundant near the coast as indicated by the following metre net records of April: sta. 30, 47 per cent; sta. 32, 74.9 per cent; sta. 33, 55.6 per cent; sta. 35, 70.5 per cent; sta. 8A, 60.5 per cent.

FIGURE 31. Distribution of *Balanus balanoides* larvae in April and May, 1932. Number per minute of towing with a half-metre net; 50 metres to the surface.

A month later in May, when cyprids dominated in the central area, spawning was centred in the inner bay on the New Brunswick coast east of Point Lepreau. In Newfoundland, *Balanus* breeds usually in June. *Cancer* zoea appear at Woods Hole and in the bay of Fundy at about the same time in May. As an example of progression to the westward, *Mytilus* larvae in 1932 appeared on Georges bank and along the southern and western coasts of Nova Scotia in April (p. 275), and in the eastern coastal area of the gulf in May (figs. 32 and 33). At Woods Hole in 1922 and 1923 they were found first in early June.

Why so few larvae of benthonic invertebrates representing such a limited number of species have been taken in the gulf and bay, even within the 100 metre contour, is an open question. The exact number of endemic species in this group

is not known because the region, particularly the offshore area, has been inadequately investigated. The extensive list of species recorded by Kindle and Whittaker (1918, pp. 228-294), however, is ample evidence that the fauna is far richer than the pelagic larvae would indicate. Larvae of but 24 species were found outside of the headlands, during the two years. Of these 15 were Crustacea, four echinoderms, three molluscs, and two annelids. In a similar period at Woods Hole, ten years before, more than 60 species of larvae were taken in plankton nets, there being approximately 36 species of Crustacea, 12 annelids, nine molluscs, one echinoderm, and one chordate. Compared with three species of crab larvae north of cape Cod, 20 were obtained at Woods Hole (Fish 1925, p. 160). The two sets of data are not exactly comparable because the latter collections were

FIGURE 32. Distribution of *Mytilus edulis* larvae in April, 1932. Number per minute of towing with a half-metre net; 50 metres to the surface.

from inland waters. However, lists covering two summers in Frenchmans bay (1929, 1930) and two summers and one winter in Passamaquoddy bay (tables XIX and XXI) are hardly more extensive than those of the open gulf. Similar conditions were also found in 13 bays visited in August 1932, and in records of McMurrich for a period of 12 months in Passamaquoddy bay (p. 286). Investigations of a different type will be necessary to determine whether a larger percentage of boreal benthonic species are viviparous, or have young so advanced upon hatching that like the lobster, *Sclerocrangon*, and some of the mysids, they immediately seek the bottom or remain in surface waters for too short a time to become very widely distributed.

Seasonal variation. The principal breeding periods of benthonic invertebrates in the region occur between April and October. There was no evidence of winter spawning in the bay of Fundy in 1931-32, although advanced larvae of two species of *Spirontocaris* were found in small numbers until early November and a single *Cancer* megalops in December. In the spring of 1932 *Eupagurus* larvae appeared in March, and by late April nine species were widespread in the bay (table XV).

FIGURE 33. Distribution of *Mytilus edulis* larvae in May and June, 1932. Number per minute of towing with a half metre net; 50 metres to the surface.

Both in species and total numbers of larvae the data indicate two maxima in the bay and central area, April-May and August-September. Since the stock appears to be made up largely of the same species in both periods, one might conclude that, as in pelagic species like *Meganyctiphanes,* spring forms in the eastern portion of the region represent migrants from the western gulf, and summer larvae, local production. In the bay of Fundy in 1932 the number of species rose from a

mid-summer low of two (*Littorina* and *Hyas*) at the only station taken in July (sta. 5) to 10 in August, with nine remaining in mid-September. The gradual decline throughout the summer in offshore waters in the western area, almost terminating by the end of August, offered further indication that the spring maximum in 1932 might have been largely of western origin. West of Mount Desert in 1931, however, stations nearer the coast in August yielded 13 species comprising 3.4 per cen of the total zooplankton population (p. 280), and in 1932 records from bays showed production in inland waters almost equally intensive in all areas (table XVIII). It seems probable, therefore, that in some species spring spawning may be restricted to the western area, but an August maximum, at least in neritic waters, occurs throughout the region.

Considering individual species, a few appeared to have relatively short spawning seasons and occurred in but one of the two periods. *Cucumaria,* and two species of *Spirontocaris* were found only in August and September. However as certain others occurring only in spring collections at offshore stations (table XV) were found in bays in August (table XVIII), further records from neritic waters may extend the seasons of the above mentioned.

Balanus nauplii appeared in the spring and again in August and September. A similar condition occurs at Woods Hole, the first stock consisting of *B. balanoides* and the second of *B. crenatus*. Adults along the coast of Maine were not examined, but pending verification, it is suggested that the second and much smaller brood in 1932 were nauplii of *B. crenatus,* a species apparently common throughout the coastal zone.

Regional variation. Too little is known about the distribution of adult benthonic invertebrates in the region to permit a determination of possible sources of young occurring in small numbers offshore. Mount Desert probably marks one of the most important faunal barriers for neritic species within the gulf (p. 284), but the differences in pelagic larvae east and west of this point in 1931 and 1932 appeared to be more quantitative and seasonal than qualitative. With the exception of *Balanus,* previously discussed on page 271, no members of the benthonic group occurred in coarser net collections in sufficient numbers to indicate production centres. The pump and half-metre nets of finer mesh, however, yielded eggs and larvae of two molluscs, one larval cirriped, and eggs of an unknown form, showing definite regional variation which differed strikingly from that of true planktonic species.

The distribution of *Mytilus edulis* larvae from April to June in 1932 is shown in figures 32 and 33. (Eggs were taken only with the pump in July and August). It will be seen that spawning in April was centred on the south coast of Nova Scotia and on Georges bank, with smaller numbers on the western Nova Scotian coast, but apparently the season had not yet begun in the bay or inner gulf. In May production extended into the bay along the Nova Scotian side and as far west as Penoboscot bay, but no larvae were found in New Brunswick waters. By June they appeared on the New Brunswick coast and at offshore stations in the eastern gulf. There was still no evidence of appreciable spawning in the western area,

although larvae from an unknown source were numerous in the drift entering the bay of Fundy. Pump samples in August 1932 indicated that propagation reached a peak at that time east of Mount Desert. In the bay eggs occurred up to 47,460 (sta. 37) and larvae to 25,780 (sta. 7) per cubic metre. The numbers were also

FIGURE 34. Distribution of eggs and larvae of *Mytilus edulis* in August, 1932. Number per cubic metre; 50 metres to the surface.

large in the eastern part of the central area, but in the western area relatively few were found except in the immediate vicinity of Casco bay where 7,397 larvae per cubic metre appeared in the shallowest station (sta. 25A) (fig. 34). The season apparently terminated in September. Records from five stations in the bay of

Fundy (September 14-16) showed no eggs at three (sta. 19, 11A and 13) in the inner part and but 197 and 187 per cubic metre at two (sta. 8A and 36) in the outer part. Larvae were taken at all stations, being most numerous (sta. 8A and 9) along the Nova Scotian coast (1,127 and 1,490 per cubic metre).

In August, 1931, eggs were centred in the central area, amounting to 17,306 per cubic metre at sta. 15, and larvae southwest of Mount Desert where 18,197 per cubic metre were taken at sta. 20 (fig. 35). The western area again appeared

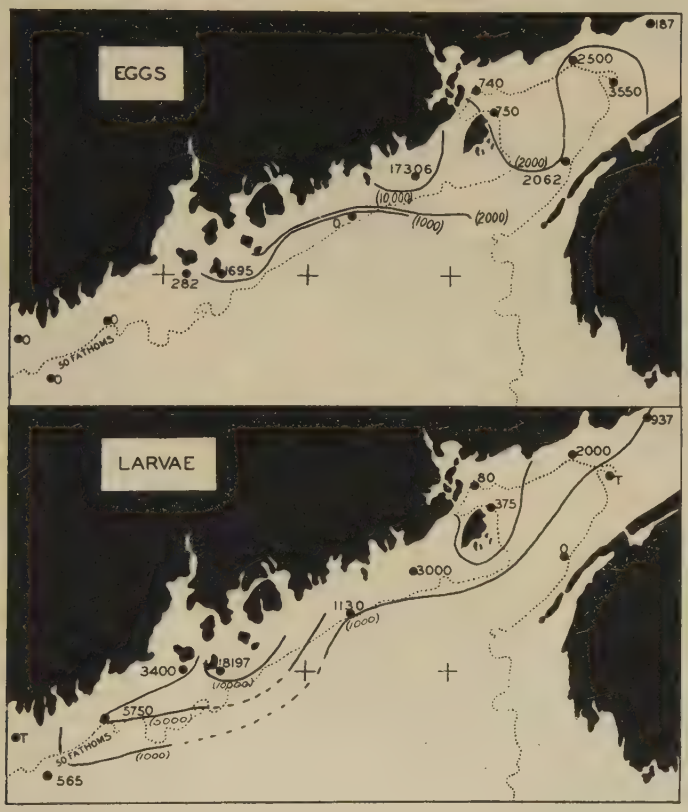

FIGURE 35. Distribution of eggs and larvae of *Mytilus edulis* in August-September, 1931. Number per cubic metre; 50 metres to the surface.

relatively unproductive, for no eggs were taken west of Penobscot bay and larvae decreased rapidly along the course of the drift from this point.

It would thus appear that from April to September in 1932, and at least in August 1931, propagation of *Mytilus* was centred in the eastern gulf and bay. The large numbers in late stages also afford ample evidence that the region offers no unusual restriction to normal development in this species. The reason for the apparent scarcity in the western area remains problematical. It is hardly likely

FIGURE 36. Distribution of eggs and larvae of unidentified pelecypod (DE) in August-September, 1931, and in August, 1932. Number per cubic metre. Eggs (937 per cubic metre) were found only at station 13 in 1932.

that their numbers could have been so greatly reduced by enemies or that spawning and the subsequent pelagic period could have passed between cruises, and yet extensive local propagation must take place at some season because adults abound about the entire margin of the gulf. As larvae south of the cape are most numerous in early June (Fish 1925, p. 137), one would expect them in the western sector of the gulf in May (p. 191). No evidence was found there of significant local propagation in 1932, either at the beginning (May 2) or end (May 21) of that month. The matter must await further investigation.

A second species of molluscan larva not positively identified (fig. 37) appeared in the pump samples during August and early September. It may prove to be *Anomia.* In 1931 these larvae were found widespread in the gulf in late August and in the bay in early September, being most abundant about Grand Manan. The distribution of eggs (0.06×0.078 mm.) at this time is shown in figure 36. In 1932 neither eggs nor larvae were taken in the gulf and in the bay the former appeared only at sta. 13 (937 per cm.) in August. Larvae, both in August and September, were restricted largely to the inner bay, in the latter month ranging up to 200 per cubic metre at sta. 9, 11A, and 13, but absent at the outer stations, 8A and 36. Like *Mytilus,* propagation in this species appeared to be centred in the eastern part of the region with smallest returns in the western area off Casco bay.

Two species appeared to originate in Nova Scotian waters. One, a cirriped larva known in the eastern Atlantic as Hensen's nauplius (Hoek 1909), was found in April off Halifax and along the west coast of Nova Scotia into the bay of Fundy. None were taken in the inner bay, or at 21 stations in the inner and outer gulf (fig. 38). In May a few appeared at one station near the mouth of the bay (sta. 34) and at one in New Brunswick waters (sta. 13). The second species, represented by eggs, (fig. 39) appeared only in April and could not be identified. It was taken in six hauls off the south coast and in one off the west coast of Nova Scotia. Its total absence elsewhere in the gulf and bay would suggest a movement into the region from the eastward, in the drift past cape Sable known to occur at this season (p. 202).

Evaluation of species. Local swarms of larvae of bottom species are frequently encountered inside of the headlands during the spring and summer, but in the open gulf and bay, except for a short period of two months, April and May, they formed a relatively insignificant part of the pelagic population in 1932. In the western area where their appearance coincides with vernal augmentation of dominant zooplankton species, they were never found exceeding 5 per cent (table V). Progressing eastward they became increasingly important at this time because of the seasonal delay in zooplankton response in the central and New Brunswick areas. In April, due largely to *Balanus* propagation, they formed 39.6 per cent in the central area and 17.6 per cent in the bay, with much higher values at some of the individual shallow stations. By May, with the passing of barnacle larvae, the values declined to 0.3 per cent in the western area, 6.0 per cent in the central

area, and 8.1 per cent in the bay of Fundy. Thereafter values exceeding 0.5 per cent were found only in the bay, and here the August maximum amounted to only 3.3 per cent. It can be concluded with reasonable certainty, therefore, that pelagic larvae of benthonic species are rarely of significance in the natural economy of the open gulf, and only slightly more important outside of the headlands in the bay of Fundy.

Not all of the larvae in the collections have been identified, particularly among the annelids, molluscs, and macrurans. Nine members of the latter group have not been determined. However, it is probable that when a more detailed study

TABLE XV. Larvae of benthonic invertebrates.

	Total region					Western area		
1932	Apr.	May	June	Aug.	Sept.	Apr.	May	June
Balanus balanoides larva	18.0	3.8				.4	.02	
Crago septemspinosus larva		.02						
Other macrura:								
Macruran A					T			
Macruran B				T	T			
Macruran B'				.07	.03			
Macruran C				.8	.2			
Macruran D	.2	.1	T			.03	T	T
Macruran E	.1	.7		T		T	T	
Macruran F	.05	.03				.06	.1	
Macruran W				T				
Eupagurus sp.	.5	.7	.4	.1	.03	.05	T	.03
Cancer sp.		T	T	.03	.1			T
Hyas coarctatus	.1	.05	.3	.7	.1	T		.2
Ensis directus (Juvenile)					T			
Lepidonotus squamatus		.03						
Nereid larva		.2						
Asterias vulgaris	.01							
Ophiopluteus	1.3	.07		T		3.9	.2	
Cucumaria frondosa	.02	.2	T			T	T	T

can be made, the identity of several of these will be revealed, because the larvae of the more common species in the region have already been described from European waters.

Between October and March occasional larvae of four species of benthonic invertebrates, described on page 274 were taken in the bay of Fundy. The relative numerical values in the different areas between April and September in 1932 are shown in table XV. Crustacea comprised the greater part of this group at all times.

In 1931 the results shown in table XVI were obtained.

Two of these species, *Carcinides maenas* and *Strongylocentrotus drobachiensis* did not appear in the collections of the following year.

In 1917, at one station in the bay of Fundy, (sta. 5) no members of this group were found in January, February, March, August, September, and December. The records for the other months represented in the collections were as follows: April, macruran C. 3.1 per cent; May, *Balanus* 0.6 per cent, macruran C. 1.1 per cent; June, *Balanus* T; July, *Eupagurus* sp. 1.1 per cent; *Hyas* 1.1 per cent; October, *Cancer* 0.3 per cent; November, *Hyas* 0.4 per cent.

In outer areas in 1932, no larvae were found at four stations off the south

coast of Nova Scotia in January, but in April eight stations in the same locality yielded, macruran C. 0.4 per cent, *Eupagurus* 0.2 per cent and traces of *Balanus* and macruran J. In May traces of macruran F. and an *Ophiopluteus* larva were taken in the central basin of the gulf, and *Balanus* (1.0%) and macruran C. (T) in the eastern channel. None appeared at one station on Browns bank. In September but one species, *Cancer* (0.9%) was found at four stations in the outer gulf, and but two species, *Eupagurus* (0.3%) and macruran A. (T), on Georges bank. No members of this group appeared in one haul off the west coast of Nova Scotia at this time (sta. A1410).

Relative percentages in metre net collections, 1932

Central area						Bay of Fundy				
Aug.	Sept.	Apr.	May	June	Aug.	Sept.	Apr.	May	June	Aug.	Sept.
		38.6	5.0				16.2	5.3			
			.03					.03			
											T
T					T					T	T
					T					.02	.1
T	T				.2	T		T		1.5	.6
		.04	.4	T			.4	.1	T		
		.3	.1		T		.1	.1		T	
		.1	.01				T	T	T		
										T	
T	T	.5	.2	.1	.2		.8	1.3	.7	.2	.1
T					.05			T		.05	.4
.06		T	T	T	.1		.2	.1	.5	1.4	.3
											T
			T					.1			
								.5			
		.02									
							.01	T		T	
		.06	.1	T			T	.5	T		

TABLE XVI. Larvae of benthonic invertebrates in zooplankton collections in 1931. Relative percentages

Area	Western	Central	Bay of Fundy
Month	August	August	September
Balanus crenatus	T	3.7	0.3
Crago septemspinosus	0.3	0.2	
Macruran A	T		
Macruran B	0.1	0.03	
Macruran C	0.8	T	0.7
Eupagurus sp	0.3	T	T
Cancer irroratus	1.5	0.1	
Carcinides maenas	T		
Hyas coarctatus	T	T	0.1
Ophiopluteus larva	T	T	
Strongylocentrotus	0.01		0.01
Littorina litorea	0.02		
Mytilus edulis	0.35	0.4	

BENTHONIC INVERTEBRATES

Too little consideration has been given to the importance, in the natural economy of the region, of the very rich fauna on or associated with the bottom. In the inner gulf and bay mysids, Cumacea, caprellids, gammarids, ostracods, and benthonic copepods, together with many less abundant forms were regularly taken whenever the bottom was sampled. Unfortunately no quantitative data are available for these waters and such studies could not be included in the present program.

Adult benthonic forms appearing in the collections may be grouped in two classes, accidental and free-swimming. Most were accidental, and had either been passively transported into the upper levels by violent current action or entered nets coming in contact with the bottom. The increasingly large numbers of both species and individuals encountered eastward from Mount Desert, with maximum

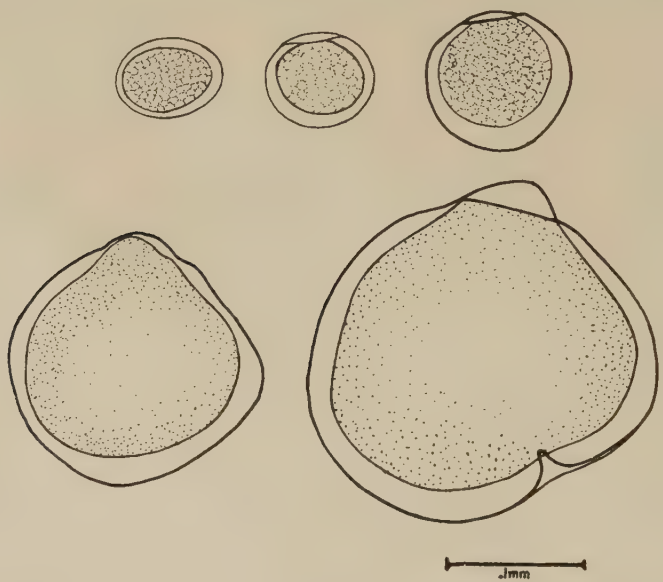

FIGURE 37. Egg and early developmental stages of an unidentified pelecypod (DE), possibly *Anomia aculeata*.

numbers in the bay of Fundy, are indicative of turbulence. Some in the central area and almost all of those in the western area were scraped from the bottom as evidenced by sand or mud in the nets. A relatively few species, the most common of which were members of the genus *Idothea,* were taken clinging to weed or other floating objects at the surface. This class of accidental forms should probably not be included with zooplankton, but the second, consisting of benthonic species free-swimming during their breeding season, can be correctly considered a part of the pelagic population.

The two groups can usually be distinguished in plankton collections. Excluding those found on drifting objects, accidental forms are most frequently represented by several and often many species in a haul, particularly when the

bottom has been touched. Breeding forms most commonly occur as single species in relatively large numbers. Neritic mysids, amphipods, annelids, and on rare occasions Cumacea have been found free-swimming in the western Atlantic. At Woods Hole swarms of amphipods (*Batea secunda, Gammarus annulatus, Monoculodes edwardsi, Stonothoë cypris,* and *Calliopius laeviusculus*), mysids (*Neomysis americana*), and annelids (*Nereis virens, N. limbata, N. pelagica, Platynereis megalops* and several species of the genus *Autolytus*), were observed in 1922 and 1923 (Fish 1925, pp. 130, 149, and 152). Such concentrations are rarely found beyond the shallow coastal zone, although *Autolytus* was at times taken well offshore in the gulf, and one species, *Calliopius,* has been reported in the vicinity of the Gulf Stream (Fish 1925, p. 150).

FIGURE 38. Distribution of Hensen's cirriped nauplius IV in April, 1932.

Thirty-eight species of benthonic invertebrates were found in the offshore collections of two years, 23 in 1931, and 28 in 1932. These comprised two macrurans, two mysids, ten Cumacea, eight amphipods, five isopods, three copepods, one mollusc, one cephalopod and six annelids. As previously mentioned (p. 273), considering the number of species reported from the bay of Fundy alone (Kindle and Whittaker 1918), it is evident that the present material is not indicative of the composition or abundance of the bottom fauna. (When sand or mud was observed in the sample, the haul was repeated. Had such collections been recorded the list would have included many more species.) It is included here merely to show that although certain species are at times pelagic, they apparently never form an appreciable part of the zooplankton population of the open gulf and bay.

Our data are also too sparse to indicate regional variation, and previous records afford little on the ranges of benthonic species. In the inner gulf, Mount Desert, where the cold drift from the eastward veers offshore, probably forms an important faunal barrier due to differences in temperature and turbulence (p. 275). Possibly other barriers, less marked perhaps and affecting fewer species, may also occur. Cape Ann and perhaps cape Elizabeth might be expected to form minor barriers, and differences in the benthonic fauna on the two sides of the bay of Fundy are observable.

Seasonal variation was evident in a few species free-swimming during the spawning period. Mature adults of *Nereis virens* were found in small numbers in the central area and also off the west and south coasts of Nova Scotia in April

FIGURE 39. Distribution of an unidentified egg (Q) in April, 1932.

1932. A month later they appeared in collections from the bay of Fundy. Of four species of *Autolytus,* three (*A. alexandri, A. cornutus,* and *A. varians*) occurred at the surface only in April and May, but a fourth, *A. longisetosus,* although most abundant in April (0.2% in the bay), was widespread over a much longer period: August (1931), January, April, May, June, and September (1932). *Neomysis americana* was found at the surface in April only. Considered by areas the pelagic periods appear, in some instances, to occur later and be more extended in the bay of Fundy. None were found in the western area after April, and in the central area after May.

At Woods Hole the breeding seasons tend to begin earlier than north of the cape, the largest swarms of breeding amphipods occurring during the winter

months (Fish 1925, p. 149), *Neomysis* from December to April (p. 152), *Nereis virens* in April (p. 131), and in the case of *Autolytus,* egg bearing adults of one or more species have been taken in every month of the year (fig. 33, p. 131).

Amphipods and cumaceans which may have been pelagic were taken in small numbers in the central area and bay in 1932, but occurring in turbulent waters together with obviously accidental forms, they could not be distinguished with certainty as such, although in some instances they were carrying eggs.

Evaluation of species. The relatively insignificant numbers of benthonic invertebrates in the zooplankton at all times is indicated by the fact that, in the bay of Fundy where the largest hauls were obtained, the values did not exceed 0.3 per cent at the periods of greatest abundance, April and June (tables IV, V and VI). The three most numerous forms in collections from the latter area were *Autolytus longisetosus* (0.2% in April). *Dulichia porrecta* (0.2% in June) and *Neomysis americana* (0.1% in April). All other species occurred everywhere as traces. The following species were taken during the two years:

TABLE XVII. Occurrence of benthonic invertebrates in zooplankton collections. Relative percentages in metre net hauls

Area	Gulf		Bay
Year	1931	1932	1931-1932
Crago septemspinosus			T
Pandalus montagui		T	
Erythrops erythropthalma	0.05	T	T
Neomysis americana	0.02		T
Campylapsis rubicunda	T		
Diastylis abbreviatus	T		
Diastylis polita		T	
Diastylis quadrispinosa		T	
Diastylis sculpta	T	T	T
Eudorella hispida		T	
Lamprops fuscata	T		
Leptostylis longimana	T		
Leucon nasicoides			T
Petalosarsia declivis			T
Anonyx nujax		T	
Calliopius laevisculus	T	T	T
Corophium cylindricum	T	T	T
Dulichia porrecta	T		T
Monoculodes sp.	T		
Podocerus sp.		T	
Stegocephalus inflatus	T		
Stenothoë cypris	T		T
Aeginella longicornis			T
Caprella linearis	T		
Cyathura brachiata	T	T	
Idothea baltica		T	
Munna kroyeri	T	T	

TABLE XVII—*Continued*

Area	Gulf		Bay
Year	1931	1932	1931-1932
Harpacticus chelifer	T		T
Harpacticus uniremis			T
Tisbe furcata			T
Dentalium entale	T		
Rossia glaucopis	T		
Autolytus alexandri			T
Autolytus cornutus			T
Autolytus longisetosus	T	T	T
Autolytus varians			T
Nereis virens		T	T
Sternaspis fossor	T		
Floating hydroids		T	T

INLAND WATERS

Zooplankton collections were obtained in sixteen bays in the gulf and Fundy regions in August and September 1932 (fig. 2). Eight Petersen trawl samples from St. Mary bay, taken by the Nova IV in December, January, and April (1931-32) are not comparable quantitatively with the plankton-net hauls, but indicate the character of the winter population in that area. Also available are unpublished data obtained by the senior author in inland waters between cape Ann and Mount Desert in August and September 1924, and weekly observations during two summers (1929 and 1930) in Frenchmans bay, with occasional records from Blue Hill and Penobscot bays.

Material from Passamaquoddy bay and the outer Quoddy region (sta. 5) includes routine collections during the period, July 1931 to September 1932 (fig. 40), and occasional data from the entering passages to Passamaquoddy bay in August and September 1931 and September 1932. From former years records were obtained of 33 hauls in the bay between November 23, 1915, and October 9, 1916, compiled by Dr. J. P. McMurrich, and 10 samples taken by the Biological Board of Canada between March 19 and December 19, 1917.

COMPARISON OF INLAND WATERS OF THE GULF AND BAY OF FUNDY

QUANTITATIVE DISTRIBUTION

Observations in August 1932 extended from Casco bay to Pt. Lepreau (sta. A-M), with two stations on the Nova Scotian coast, in St. Mary bay (sta. J) and Annapolis basin (sta. K). The neritic population at this time showed the same quantitative decline to the eastward as the offshore population (fig. 41), the highest value (151 cc.) being obtained in Casco bay. In the vicinity of Penobscot bay the volume was 93 cc., in Frenchmans bay 53 cc., off Pleasant bay 12 cc., and Machias bay 9 cc.

Quantitatively the population in neritic waters throughout the region was

smaller than in neighbouring offshore areas, a condition also observed by Bigelow (1926, p. 85). During the summers of 1931 and 1932 volumes never failed to decrease upon approaching the coast and within bays the quantities were small compared with those in the vicinity of the entrances. Thus upon entering Penobscot bay in August the volume decreased from 93 cc. to 44 cc., and in Frenchmans bay from 53 cc. to 8 cc. No station was made off Blue Hill bay, but

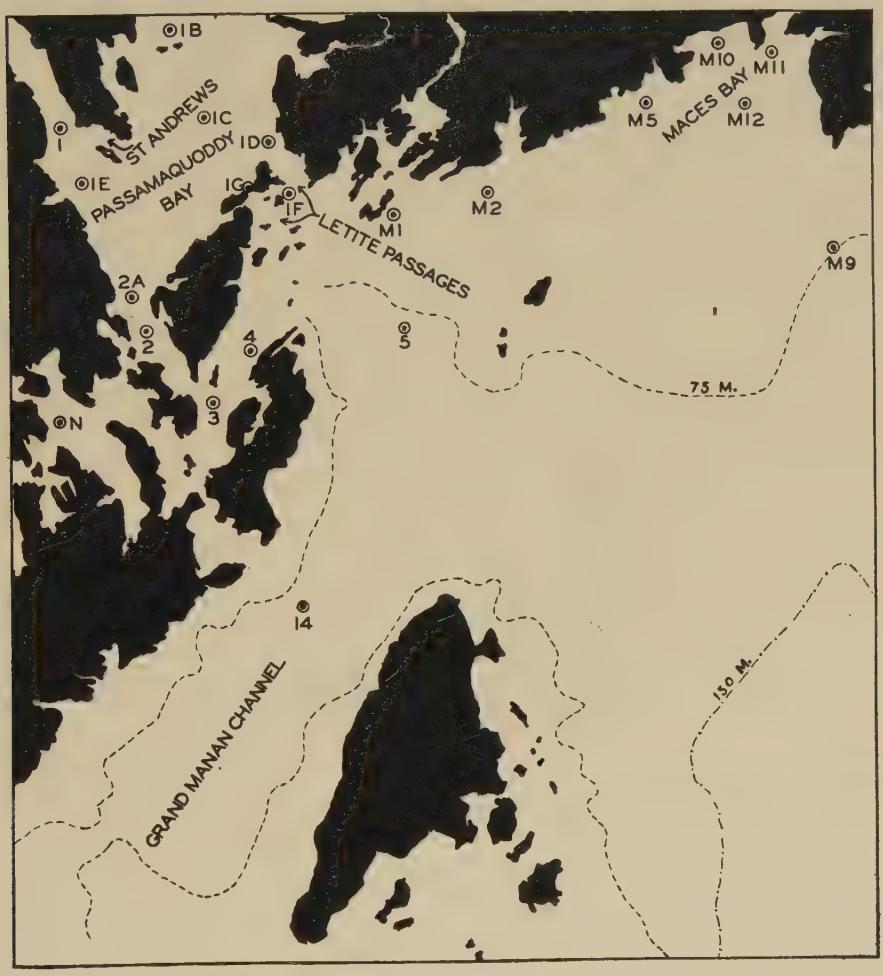

FIGURE 40. Zooplankton stations in the vicinity of Passamaquoddy bay.

one between Swans island and Bass harbour in the bay proper, yielding only 19 cc., indicated conditions comparable with the others. In the bay of Fundy volumes declined from 46.9 cc. in the outer Quoddy region (sta. 5) to 20 cc. in Passamaquoddy bay (fig. 41), and from 44 cc. at sta. M9 to 10.5, 9.3, and 6.5 cc. at stations M10-12 in Maces bay (fig. 40).

COMPOSITION OF THE POPULATION

Records from Frenchmans bay in 1929 and 1930, and in Passamaquoddy bay in 1931 indicate propagation of neritic zooplankton to be at a maximum in mid-August when the present collections were made.

Considering first the ecological groups comprising the population, all but one (southern migrants) of those found in the open gulf were represented in inland waters, although as shown in table XVIII northern migrants did not appear west of Mount Desert at this time. Physical conditions, particularly depth, temperature, and stability, vary greatly in different localities and result in corresponding variations in the character of the zooplankton, even in neighbouring bays (tables XVIII and XIX). Areas having marked thermal stratification were found to contain the richest summer populations, with boreal offshore forms concentrated by day in the cold bottom water, neritic species at intermediate depths, and eggs and larvae in the warm upper layer.

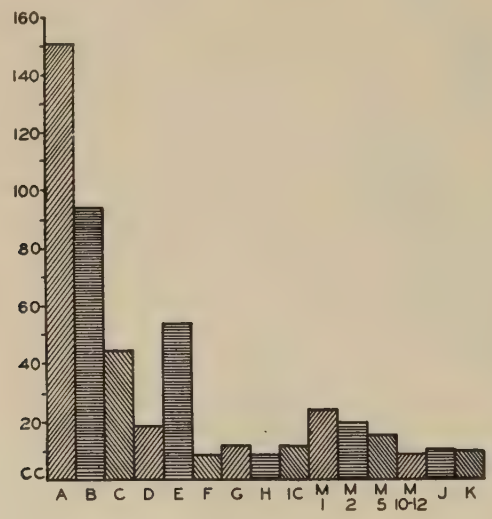

FIGURE 41. Comparative volumes (displacement) at neritic stations in August 13-19, 1932. Twenty minute oblique metre net hauls.

Open gulf species form a considerable part of the stock throughout the year, but as in the outer coastal zone, regional differences are greatest in summer. At that time in the stable western area cold water persists in the lower levels of the deeper bays, and here members of this group remain in relatively large numbers. At all stations west of Mount Desert in August 1932 they exceeded 60 per cent of the total population except in the shallower part of Penobscot bay, and there the values quickly rose from 26.2 to 83.2 per cent at the entrance. In Frenchmans bay turbulence reduces the temperatures in the upper levels, but does not seriously affect the bottom water, which warms very slowly during the late summer. There were therefore, relatively few larvae of offshore species (p. 311) but adults even in the inner part near Ironbound island on August 15-16 amounted to 79.4 per

cent, almost as high as off the entrance (83.6%). Passing eastward from Pleasant bay (sta. G) there was a marked decline in offshore species in the very turbulent central and New Brunswick areas. In Machias bay (sta. H), with a surface temperature of 10.5°C. and a vertical gradient of less than 1°C. in 40 metres, they formed only 31 per cent, and in Passamaquoddy bay 27 per cent. Along the New Brunswick coast, except for local swarms of *Meganyctiphanes* eggs encountered off the L'Etang river (sta. M1) and at some of the stations in Maces bay (sta. M5 and M12), the boreal stock was comparable with Passamaquoddy and Machias bays, totalling 14 per cent in Mink bay (sta. M10) and 32 per cent in Lepreau bay (sta. M11). Representative of very shallow areas where the entire water mass responds to summer warming, members of this group in St. Mary bay (sta. J) and Annapolis basin (sta. K) were very sparse, as indicated in table XVIII.

TABLE XVIII. Composition of the zooplankton population in neritic waters. Relative percentages

Region	Western area					Central area							New Brunswick area					Nova Scotia	
Station	A	B	C	D		E	F			G	H		1C	M1	M5	M10	M11	J	K
Year	1932	1932	1929	1932	1927	1932	1932	1929	1930	1932									
Date - August	13	14	20	14	20	14	15	3	16	9	15	15	21	15	17	18	18	16	19
Open gulf species	82.3	83.2	55.8	26.2	44.7	61.6	83.6	41.6	60.2	79.4	65.1	31.0	27.0	92.4	98.9	14.0	32.7	24.4	9.9
Northern migrants							T		T				T	.3					
Neritic zooplankton	6.4	14.8	2.5	55.8	6.4	32.2	11.0	37.2	36.4	5.6	13.8	41.5	68.2	7.2	.7	80.4	66.5	42.2	61.8
Fish eggs & larvae	8.1	1.0	38.8	.6	44.6	3.4	3.0	15.2	T	11.4	9.5	1.5	1.0	.2	.5	1.8	.7	4.4	2.5
Larvae of benthonic invertebrates	3.1	.8	2.8	17.4	3.4	2.5	2.7	5.9	3.2	4.0	11.9	25.5	3.6	.1	.2	3.7	T	28.4	26.0
Benthonic invertebrates			T			T			T		T	.4				T	T	.6	

Neritic species and larvae of benthonic invertebrates attained their highest values in shallow enclosed bays such as Penobscot (73.2%), St. Mary (70.6%), and Annapolis basin (87.8%), and in turbulent waters like Machias bay (67%), Mink bay (85.1%), and Lepreau bay (66.5%). It would appear, however, that these two groups reproduce successfully in bays throughout the region, the relatively large percentages in shoal and turbulent waters being due for the most part to the decrease in offshore species, as indicated clearly by the smaller volumes in those areas.

Pelagic fish eggs and larvae were least abundant in New Brunswick waters (0.8% average) and the eastern part of the central area (1.5%). They increased rapidly to the westward, forming 9.5 per cent in Pleasant bay and 11.4 per cent in Frenchmans bay. The actual numbers were even larger farther west, but due to the much richer invertebrate population, the average percentage for the four stations, A to D, amounted only to 3.3 per cent.

Former August records show wide variations from year to year in some of the bays (table XIX). In almost every case this resulted from differences in the propagation of a very few species. For example, in Penobscot bay in 1929 small numbers of six neritic plankton species totalled 2.9 per cent with no one exceeding 0.8 per cent, while in 1932 two species, *Phialidium* and *Podon leuckarti*, amounted to 54 per cent. In Blue Hill bay the latter species in 1932 formed 28.4 per cent of the total of 32.2 per cent for the group, but was absent in 1929. In French-

mans bay, although *Podon polyphemoides* was not found in 1932, it swarmed both in 1929 (59% on August 3) and 1930 (73.7% on August 7, and 69.6% on August 16). Similarly the large percentages of fish eggs and larvae in 1929 in Penobscot bay (38.8%) and Blue Hill bay (44.6%) consisted almost entirely of *Merluccius* and *Tautogolabrus* which appeared as traces in 1932. It is probable that in most instances these records do not indicate annual quantitative differences, but rather

TABLE XIX. Evaluation of species comprising the

Year	1932							
Area	Western				Central			
Station	A	B	C	D	E	F	G	H
August	13	14	14	14	15	9	15	15
Calanus finmarchicus	14.3	39.2	4.2	7.3	35.6	3.5	33.8	9.3
Metridia lucens	23.6	6.0	.6	2.1	23.8	3.5	10.3	1.1
Pseudocalanus minutus	2.0	.2	3.0	4.7	10.7	10.9	2.8	17.4
Centropages typicus	1.0	8.1		.4	.3		2.4	
Meganyctiphanes egg		21.8			4.2	46.2	.4	.7
N. norvegica larva and adult	40.6	6.3	2.4	2.2	2.1	1.8	2.4	
Sagitta elegans	T	.2	11.8	19.0	2.4	9.6		T
Oikopleura labradoriensis				.9	T		2.8	1.1
Fritillaria borealis		.5	.6		3.9	3.0	10.2	.7
Temora longicornis	.2		.6	13.8		.9	T	.7
Limacina retroversa	.6		2.4	8.2				
Thysanoessa, young	T	.5	.6	3.0	.6	T		
Aglantha digitalis	T	.2			T		T	
Acartia bifilosa								
Acartia clausi								2.8
Acartia longiremis			.6	.4		.4	.4	T
Centropages hamatus			T					
Eurytemora herdmani		.2	T	3.4	.3			.7
Tortanus discaudatus	.4		T	T		1.3	2.8	8.5
Evadne nordmanni	.2	12.5			1.5		3.5	
Podon leuckarti			19.1	28.4	8.6	3.5	6.7	28.8
Podon polyphemoides								
Obelia sp.	5.4		1.2	T	.6		.4	.7
Phialidium languidum	.4	2.1	34.9		T	.4	T	
Enchelyopus-Merluccius egg	7.1	.5	.6	3.0	1.2	11.4	7.9	1.1
Gadus-Glyptocephalus egg	.6	.5		T	1.5	T		T
Glyptocephalus cynoglossus larva	.4	T			.3		1.6	
Limanda ferruginea egg		T	T	.4	T		T	.4
Tautogolabrus adspersus egg								
Calliopius laeviusculus								
Balanus crenatus nauplius				.4		.9	3.9	6.7
Crago septemspinosus larva								
Macruran B larva	.9			.4	.9	2.2	2.8	9.9
Macruran C larva		T	8.4	1.3			.8	
Eupagurus sp. larva	T		T					1.8
Cancer irroratus zoea	2.2	.8	5.4	.4	.9	.9	2.0	1.8
Lepidonotus squamatus larva								
Asterias vulgaris larva			3.6		.3			
Mytilus edulis larva								
Littorina litorea egg and larva							2.4	5.3

variations in the period of the maxima, as in the case of *Acartia* in Passamaquoddy bay (p. 294). However, common neritic species have frequently remained sparse and sometimes apparently absent in certain years. The above mentioned form, *P. polyphemoides,* was widespread in the western and central areas in two former years, but in 1932 it was not taken anywhere in the region. Another member of the genus, *P. leuckarti,* did not occur in 33 hauls in July and August in French-

mans bay in 1929 although it proved abundant at that season in 1930 and 1932. A third species, *P. intermedius,* was observed only at Boothbay harbour, where on August 31, 1932, a swarm was so dense that the water appeared cloudy and more than three ounces (ca. 80 cc.) were taken in a single dip with a hand net. This form occurs regularly south of cape Cod in summer (Fish 1925, p. 139) and has been reported once from St. Andrews (MacDonald 1912) but did not

zooplankton in certain inland areas. Relative percentages

							1929			1930	1931
New Brunswick					Nova Scotia		Western		Central		N.B.
1C	M1	M5	M10	M11	J	K	C	D	F	F	1c
21	15	17	18	18	16	19	20	20	3	16	13
3.7	7.3	.9	2.1	5.4	1.2	1.2	2.8		.4	9.4	5.4
.2	.4		.6	.7							
9.5	4.0	1.7	5.8	16.8	T	8.7	18.5	7.8	.8	39.2	1.6
5.1	T	.7	2.8	2.7	T						
1.7	80.7	95.6	.9	.7					36.6	4.2	
1.5	T		.3		.6					T	
T		T			T		1.5	.9	.4	.1	.5
						T					
2.2		T	1.5	6.4	21.4						
2.9				T	T	T	33.0	35.4	3.4	6.9	.4
.2											
					1.2	T	T				
								3.3	2.3		
33.1	1.3		9.2	.7	6.2	49.5				.3	51.7
							.8		.8	11.6	
					10.7	2.5					
5.3	.3		T			4.9	.5		.8	.1	1.6
22.8	2.0		T	.7	12.9	4.9	T			T	7.8
3.6	2.0	.7	50.1	63.4	.6		.5	.6	3.8	.8	
2.2	1.5		20.8	1.7						.8	
				T			.5	2.5	29.5	22.8	
1.2			.3	T	11.8	T				T	
	,1						T	T			
1.0	.1	.5	1.5	.7	1.1		19.4	7.6			1.6
T	.1		.3	T		T	5.5		15.2	T	
				T	3.3	2.5					
							13.9	37.0		T	
											7.4
						1.2	T				
							2.8	T	.4	1.2	15.8
1.9	T		.6		4.5	8.7					2.6
.5				T							
.2									T		2.6
.5	T		2.8	T	2.5	2.5		3.4	.4	T	T
						2.5	T		T		
								T	.7		
							T	T	3.7	2.0	
	T		.3		21.4	11.1		T	T		

appear in collections of six years (1916, 1917, 1924, 1929-31) from inland waters of the gulf and Fundy regions.

Although varying in season distribution in different bays and to some extent in the same locality from year to year, the above records and others which may be cited indicate that the more important neritic zooplankton species have but one major propagation period, in summer or autumn. The swarms of individual

species frequently encountered at such times are usually of rather limited duration and geographical range. *Evadne nordmanni* in 1924 was found swarming in Boothbay harbour on September 3 and in Northeast harbour on September 19. In 1929 it formed up to 69.6 per cent of the population at a few stations in Frenchmans bay on July 23, and 37.8 per cent at one station in Penobscot bay on August 23, 1930. In 1932 the only swarms noted were at sta. M10 (50.1%) and sta. M11 (63.4%) in Maces bay on August 18. Another species, *Eurytemora herdmani,* formed over 80 per cent of the population in Somes sound (Frenchmans bay) on September 19, 1924, and 46.4 per cent in Passamaquoddy bay on September 23, 1932. Other swarms observed include *Acartia bifilosa* (79% on July 16, 1929, and 64.8% on July 14, 1930), *A. longiremis* (41.3% on August 12, 1930) in Frenchmans bay, and *Tortanus discaudatus* in Passamaquoddy bay (25.3% on October 15, 1931, 22.8% on August 21, 1932, and 66.8% in October 1917). A swarm of *Aurelia aurita* planulae was observed off Bluff island in Casco bay on August 29, 1924, but could not be sampled reliably with the nets in use at the time.

Evaluation of species. In table XIX are listed species comprising more than one per cent of the population in one or more neritic areas in August 1932. The distribution of open gulf forms in inland waters during the warm season is reasonably well indicated, but in the absence of seasonal data from most of the bays it is not possible to determine with any degree of certainty regional variation of neritic zooplankton species having resting stages, invertebrate larvae, or fish eggs and fry, because of possible differences in the periods of augmentation.

In regard to the genus *Acartia,* the three species *A. clausi, A. bifilosa,* and *A. longiremis* no doubt occur to some extent throughout the region but there appear to be some differences in their centres of abundance. The numbers of *A. clausi* in Passamaquoddy bay both in 1931 and 1932, as well as in Maces bay, St. Mary bay and Annapolis basin, show it to be a very important member of the neritic population in the Fundy region. In August, 1932, it was not taken west of Machias bay, or in Frenchmans bay in 1929, although in 1930 it occurred sporadically in the latter area during July and August. From Mount Desert westward *A. clausi* tends to be replaced by *A. bifilosa.* Having its maximum in July this species was not found anywhere in mid-August 1932, but in July 1929 it formed up to 79 per cent in Frenchmans bay and 69 per cent in Blue Hill bay. Again in July 1930 values as high as 64.8 per cent were obtained in the former locality. *A. longiremis* has a more extensive season and is generally more widespread in the open gulf than the other two members of the genus, but in inland waters its centre of abundance in summer appears to coincide with that of *A. bifilosa,* with a possible maximum in early August. In 1932 it was taken in small numbers westward from Machias bay and in 1930 formed up to 41.3 per cent of the population at several stations in Mount Desert waters on August 12.

In addition to those listed in table XIX the following species were taken in small numbers in August 1932:

Boreal species

Anomalocera patersoni (central and Nova Scotian areas)
Clione limacina (all areas)
Euthemisto compressa (central and Nova Scotian areas)
Halithalestris croni (New Brunswick area)
Oithona plumifera (western and central areas)
Oithona similis (western and central areas)
Pleurobrachia pileus (western area)
Stephanomia cara (western and New Brunswick areas)
Tomopteris catharina (western and central areas)

Northern immigrants

Calanus hyperboreus (central area)
Metridia longa (New Brunswick area)

Neritic species

Thalestris longimana (central area)
Melicertum campanula (western area)
Sarsia sp. (central area)

PASSAMAQUODDY BAY

Special attention was accorded Passamaquoddy bay because of its part in the problem confronting the commission (p. 190). Continuous observations, however, could not be obtained because of the other areas included in the program, but it is believed that the available data indicate reasonably well the size and character of the zooplankton population.

VOLUME OF PLANKTON

We have already commented on midsummer volumes in Passamaquoddy bay, which, in common with those of other bays in the barren eastern coastal region, were relatively small compared with inland waters west of Mount Desert (fig. 40) and adjoining waters outside of the headlands (p. 286). Figure 42 shows the latter condition to have persisted at other seasons, the volumes being generally scantier than at station 5 which was itself usually relatively barren compared with station 6 off Grand Manan and station 8A in the path of the entering drift from the gulf.

A combination of environmental conditions apparently accounts for the small volumes characterizing Passamaquoddy bay. Added to the fact that this bay opens into a relatively barren coastal area, during the late autumn and winter months when the local environment would seem to be most favourable for offshore species, the available source of supply in outer waters is approaching a minimum. Later, judging from conditions in the early summer of 1932, the water warms and the winter (offshore) stock declines in Passamaquoddy bay before the influence of vernal augmentation becomes appreciable. Volumes in May, June, and July were smaller than in December and January (table XX). Maximum volumes,

representing propagation by the endemic neritic stock, were found in August and September (1931) at a time when the offshore population in the bay of Fundy had declined greatly from its June maximum (fig. 18).

Typical of neritic localities there appear to be marked variations in the endemic population of Passamaquoddy bay from year to year. In 1931 the dominant summer species, *Acartia clausi,* formed between 50 and 95 per cent of a population averaging 132 cc. in August and 150 cc. in September. In 1932 volumes amounted to only 4 cc. in July, 20 cc. in August, and 36 cc. in September with *A. clausi* never exceeding 33.1 per cent of the stock.

An indication of the interval of time required for local response to quantitative changes in outside waters is seen in the autumnal maximum of *Centropages typicus.* This maximum was reflected in Passamaquoddy bay, but on a very much reduced scale. In 1931 with volumes of 632 cc. in September and 274 cc. in October in the outer Quoddy region (sta. 5), values within the bay amounted to

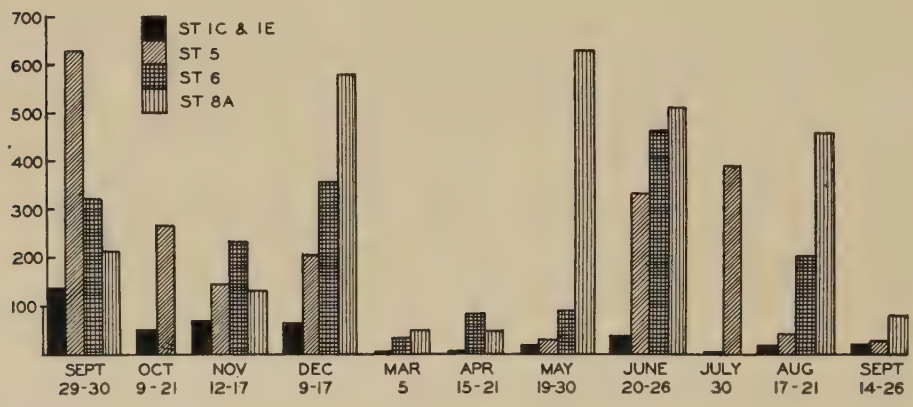

FIGURE 42. Comparative volumes (displacement) in Passamaquoddy bay and the bay of Fundy in 1931-1932. Monthly averages; 20 minute metre net hauls.

only 150 cc. in September and 57 cc. in October (fig. 42). Had the large stock remained in the outer region it is probable that the volume in the bay would have continued to increase, but the interchange appears to be so gradual that the supply in the former locality was depleted before any degree of equalization could be attained. Hence it would appear that, unless conditions following quantitative changes in the fauna of outer Quoddy waters remain fairly constant for some time, only a very limited response can be expected in the inner bay. This matter will be referred to again in considering the passages.

COMPOSITION OF THE POPULATION

Like other inland waters of the region, the zooplankton population in Passamaquoddy bay is composed of the same ecological groups found in the open gulf and bay of Fundy, but the seasonal variations in the relative size of these groups are more extreme. Again the typically coastal groups, comprising neritic plankton

species and larvae of benthonic invertebrates, at times assume far greater importance than in offshore waters.

The open gulf group is always present and for a greater part of the year dominates. The extent to which Passamaquoddy bay is populated by these recruits from outside waters is indicated by the mean of 68.8 per cent for the year 1931-32 and monthly averages ranging from 60.4 to 98.5 per cent between October and the end of June (table XX). Only in the spring (April-May) and late summer (July-October) does there appear to be sufficient local propagation (neritic zooplankton and larvae of benthonic forms) to constitute an appreciable part of the stock.

Northern migrants probably occur more frequently in Passamaquoddy bay than in neritic waters farther west in the gulf. As the two most common members of this group, *Calanus hyperboreus* and *Metridia longa,* are present in small numbers throughout a greater part of the year (p. 247) in the bay of Fundy, occasional specimens may be expected to enter Passamaquoddy bay at any time, but more particularly during the winter months. McMurrich observed *C. hyperboreus* but

TABLE XX. Composition of the zooplankton population in Passamaquoddy bay. Monthly averages; metre net collections

Year	1931-1932											1917					
Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	May	June	July	Aug.	Sept.	Mar.	Apr.	May	Oct.	Nov.	Dec.
No. of hauls	2	2	4	8	4	2	1	1	1	1	1	1	2	2	2	2	1
Volume (settling) cc.	132	150	57	56	61	63	25	47	4	20	36						
Open gulf species	7.9	3.3	60.4	97.9	97.7	98.5	66.5	91.8	49.1	27.0	29.9	87.0	8.6	.3	31.1	55.7	100.0
Northern migrants	T	T	T	T	.6		8.4			T				.1		T	
Southern migrants				T	T												
Neritic species	61.1	95.9	38.2	1.3		1.5	11.6	8.3	43.5	68.2	69.9	10.0	2.5	.9	67.0	35.6	
Fish eggs and larvae	1.6	.1	T	.2	1.8	T	1.7	T	2.8	1.0	T						
Larvae of benthonic forms	21.5	T	1.4	T	T		11.7	T	4.6	3.6	T	3.0	89.0	98.2	.7	T	
Benthonic invertebrates	7.9	T	T	.2					T						1.3	8.6	

once in winter plankton collections of 1914-15 (Willey 1921). In was comparatively numerous on February 23, 1917, sparse (1 specimen) on November 2, 1916, and on March 25, 1920 (2 specimens). Traces were found in each month from August to November in 1931 but none appeared in 1932. *M. longa* was reported by Willey (1921) on December 8, 1916, (1 female) and February 23, 1917 (scattering males and females). In *Prince* collections from the latter year it was also present in May and November. In 1931-32 it appeared sporadically at all seasons, reaching a peak of 8.4 per cent in May (table XXI).

Only those southern forms which survive for some time in boreal waters would be expected to enter Passamaquoddy bay. With so gradual a rate of interchange through the Quoddy passages (pp. 294 and 301) all but the most resistant species probably perish before reaching the inner bay. No previous records of southern species were found, and none were taken during the summer months of 1931 and 1932. However a single specimen of *Candacia armata* appeared in November and a single *Sagitta serratodentata* in December of the former year. Both are relatively hardy species occurring well into the winter in outer Fundy waters (p. 251).

Neritic zooplankton species comprise the second most important group in Pas-

samaquoddy bay, with a yearly mean of 27.2 per cent in 1931-32. Small numbers have been reported over a wide period, but they are predominately summer and autumn forms with relatively short seasonal maxima in the region. In 1931 they formed 61.1 per cent in August, 95.9 per cent in September and 38.2 per cent in October. They were relatively less numerous in 1932, amounting to 43.5 per cent

TABLE XXI. Evaluation of species in metre net

Year	1931-1932						
Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	May
Calanus finmarchicus	5.4	.5	9.5	22.3	35.4	27.0	30.0
Pseudocalanus minutus	1.6	1.8	3.1	6.5	39.5	51.4	28.4
Acartia clausi	51.7	94.2	12.9	1.2			T
Centropages typicus		.2	44.8	49.1	13.8	9.0	
Tortanus discaudatus	7.8	.3	25.3	T			6.6
Eurytemora herdmani	1.6	.6					
Pleurobrachia pileus			T	17.2	3.0	6.6	
Balanus balanoides							8.4
Euphausiid egg		T					3.3
Crago septemspinosus	15.8	T	.8				
Metridia longa		T	T		.6		8.4
Metridia lucens		T		1.4	2.5	3.7	
Acartia longiremis				.06		1.5	5.0
Sagitta elegans	.5	T	.01	.2	.4	T	
Evadne nordmanni		.3					
Podon leuckarti		T					
Podon polyphemoides		.6					
Thysanoessa young							5.0
Temora longicornis	.4	.8	3.0	.2	T	T	
Tomopteris catherina		T		T	1.4	T	
Stephanomia cara			T	.2	.9	T	T
Clione limacina				.3	.8	.8	
Meganyctiphanes norvegica		T	T		T	T	
Fritillaria borealis				.5	T	T	
Obelia sp.					T		
Cucumaria frondosa larva							3.3
Eupagurus sp. larva	2.6						T
Macruran C. larva	2.6	T					
Macruran B larva							
Macruran A larva	.5	T		T	T		
Cancer sp. zoea	T	T	T	T			
Hyas coarctatus zoea							
Enchelyopus cimbrius egg	1.6	.1					
Gadus-Glyptocephalus egg		T	T	.2	1.8	T	
Gadus-Melanogrammus egg							1.7
Urophycis chuss egg							T
Calliopius laevisculus	7.4	T	T	T			
Neomysis americana		T	T				
Autolytus longisetosis	T	T	T	.2	T		
Littorina litorea		T	.6	T			
Aglantha digitalis				T	T		T
Limacina retroversa							
Euchaeta norvegica		T	T	T			
Euthemisto compressa			T	T	T	T	
Halithalestris croni		T	T	T	T	T	
Calanus hyperboreas	T	T	T	T			

in July, 68.2 per cent in August and 69.9 per cent in September. In 1917 values of 67 per cent were obtained in October and 35.6 per cent in November, but as in 1931 (table XX) the group had practically disappeared by December.

Three species, *Acartia clausi, Tortanus discaudatus,* and *Eurytemora herdmani,* comprise the bulk of the neritic stock. The dominant species, *A. clausi,*

appears to have two generations each year, the maximum of adults occurring with the maturing of the second brood in August and September. The presence of copepodite stages (2, 303 per minute) on June 20, would appear indicative of a first generation and nauplii (79,413 per cubic metre) on July 30, of a second (table XXII). *T. discaudatus,* second in importance, may also have two, although

collections in Passamaquoddy bay. Relative percentages

				1917					
June	July	Aug.	Sept.	Mar.	Apr.	May	Oct.	Nov.	Dec.
7.1	2.8	3.7		82.0	7.2	.1	23.7	52.9	93.4
84.7	2.8	9.5	12.1	1.0	1.3	.2	4.2	1.6	
4.2		33.1	17.1		1.5	.4			
	T	5.1	15.7						
1.5	39.4	22.8	6.4	6.0	.7	.5	66.8	35.1	
1.3	.9	5.3	46.4		.3	T			
				3.0	89.0	98.2			
	42.6	1.7	.7						
	3.2								
		T				.1		T	
T	T	.2							
				4.0				.5	
T	T	T		3.0	T	T	.9	..7	6.7
	.9	3.6							
.8	T	2.2	T						
			T						
		2.9	1.4	1.0	.1		1.5	.5	
		T							
	.9								
		T							
	T	1.5							
		2.2							
.5		1.2	T						
T									
		.2	T						
		.5			T		.7		
		1.9	T						
	1.4	.5	T						
T	T	.5						T	
	2.3								
		T							
T	.5								
T		1.0	T						
	T								
	T							4.8	
			T				1.3		
		.2	T						
T						T			
						T			

this has not been definitely established. In 1932 it formed 39.4 in July and declined to 6.4 per cent in August. Later adults rose from 0.3 in September to 25.3 per cent in October 1931, and to 66.8 in October and 35.1 per cent in November, 1917. This would suggest two generations with a developmental period of approximately two months as in *Calanus, Pseudocalanus,* and *Oithona similis*

(Fish 1936a, 1936b and c). However, as the total volume of zooplankton diminished with the decline of *Acartia,* the fluctuations in the case of *Tortanus* may only be apparent and result from a somewhat longer period of adult life.

E. herdmani, which was found swarming on occasions in bays of the gulf (p 292), never assumed that importance in Passamaquoddy bay during the period of the present observations. For the most part it occurred in small numbers, but in September 1932 reached 46.4 per cent. During the previous year it averaged 1.6 per cent in August, 0.6 per cent in September and thereafter appeared to have been absent until the following June.

Larvae of benthonic invertebrates are of spring and summer occurrence, reaching peaks in April-May (98.2% in 1917) and August (21.5% in 1931). With the breeding season in most species extending over a relatively long period (p. 270), concentrations of large size are rarely found. An exception occurs in the case of *Balanus balanoides,* whose breeding period varies greatly in different localities (p. 271), but in any one area is relatively restricted. Nauplii in Passamaquoddy bay appear in March and swarm in April and May. No very high percentages were found in 1932, the greatest being 8.4 per cent in May, but in 1917 they ranged from 3 in March to 89 in April and 98.2 per cent in May. A second species, *Crago septemspinosus,* appeared from July to October and reached a peak of 15.8 per cent in August, but no other larvae of this group exceeded 3 per cent at any time.

There was no evidence that adult benthonic invertebrates are ever of significance in the zooplankton association in Passamaquoddy bay. Nets coming in contact with the bottom invariably encountered a variety of Cumacea, amphipods, isopods, mysids and other forms existing on or adjacent to the bottom, but such hauls were discarded and only species pelagic at the time of capture recorded. For the most part these occurred as single specimens probably accidentally transported upward by turbulence or attached to some floating object. The sexual stage of *Autolytus longisetosus,* however, was definitely free-swimming at the time of capture and occurred in small numbers from August to December in 1932. In October 1917 it formed 1.3 per cent of the haul. *Calliopius laeviusculus* and *Neomysis americana* were also found in small pelagic swarms. Both of these species are regularly found at the surface during the breeding season in other localities (Fish 1925). There are a few other benthonic forms in the region which are known to be pelagic at times, but did not occur in the present collections. It would thus appear that normal turbulence is not sufficient to maintain benthonic species in the upper levels in Passamaquoddy bay, and those torn from the bottom during storms quickly settle after the water subsides.

Pelagic fish eggs and larvae, as in outer waters, differ from the young of invertebrates in the region in that they occur to some extent throughout the year. They were present in very small numbers in Passamaquoddy bay, however, having a mean value of but 0.8 per cent in the zooplankton population for the year 1931-32. The highest monthly values occurred in July (2.8%) and August (1.0%)

in 1932, and August (1.6%) and December (1.8%) in 1931 (table XX). Approximately ten species are represented in the collections of the two years.

Evaluation of species. Eight species at all times (with one exception, 68.1% in August, 1931) in 1931-32 and 1917 were found to comprise more than 75 per cent of the population (table XXI). Of these, four (*Calanus finmarchicus, Pseudocalanus minutus, Centropages typicus,* and euphausiid eggs) represent boreal offshore species, three (*Acartia clausi, Tortanus discaudatus,* and *Eurytemora herdmani*) are neritic, and one (*Balanus balanoides*) is the larva of a benthonic invertebrate.

Fifty-nine other species were taken during the period of the observations but were rarely found numerous. Only a few at any time exceeded 5 per cent. Of these *Pleurobrachia pileus* formed 17.2 in November and 6.6 per cent in January. *Sagitta elegans,* another boreal species, amounted to 6.7 per cent in December 1917. A local swarm of the northern migrant, *Metridia longa* entered the bay in May 1932 and for a short time ranged up to 8.4 per cent in the small population present at the time. On another occasion the amphiphod *Calliopius laeviusculus* formed 7.4 per cent of a haul in August 1931. Occasional swarms of other neritic and benthonic species may be expected at times but these are probably sporadic and of short duration.

The following additional species occurred in very small numbers in Passamaquoddy bay (1931-32 unless otherwise noted).

Aeginella longicornis, Sept.
Ammodytes americanus, May
Anomalocera patersoni, Sept., Aug.
Candacia armata, Nov.
Centropages hamatus, Oct. (1917)
Clupea harengus larva, Oct.
Corophium cylindricum, Sept.
Cyclopterus lumpus, young, Sept.
Diastylis sculpta, Aug.
Enchelyopus cimbrius, larva, Oct., June, July
Erythrops erythropthalma, Nov. (1917)
Glyptocephalus cynoglossus, larva, Oct.
Hippoglossoides platessoides, egg, May
Hybocodon prolifer, April, May (1917)
Lumpenus lampetraeformis, young, July
Melanogrammus aeglifinus, young, July
Oikopleura labradoriensis, Dec., Oct. (1917)
Oithona plumifera, Oct., Dec., Jan.
Phialidium languidum, Oct., July
Sagitta serratodentata, Dec.
Thysanoessa inermis, Sept., Nov., Dec.

Because seasonal variations in the composition of the population in Passamaquoddy bay are of far greater magnitude than in offshore waters, the annual cycle must be considered in evaluating species. It will be seen in table XXI that the population consists in general of a winter group (November until April) derived from outside waters, but with *Pseudocalanus* assuming somewhat greater relative importance in Passamaquoddy bay; a spring augmentation of *Balanus balanoides* larvae from March until May; a gradual replacement by neritic species in late June and July (table XXII); and an autumnal invasion of *Centropages typicus* in

September which dominates until the winter stock is again recruited from the bay of Fundy with the cooling of the waters.

Considering local propagation in Passamaquoddy bay, with the possible exception of *Pleurobrachia pileus,* which appears in very early stages in late October and grows rapidly until it often forms the bulk of the collections, no winter propagation of invertebrates was observed, and the remainder of the boreal stock is believed to consist of immigrants (Fish 1936a, 1936b and c).

The benthonic invertebrate stock is no doubt to a large extent of local origin, although late stages of some of the decapods such as *Cancer* and *Hyas* were rarely taken.

The neritic stock is also probably largely endemic with one or at most two broods a year. In the case of the greater number of species, including the higher crustaceans, there is not more than one. Some of the neritic copepods, as previously mentioned (p. 298), show evidence of two, the larvae, probably developing from winter eggs, appearing some time before the adults (table XXII). Thus *Temora*

TABLE XXII. Decline of the winter population and rise of the endemic neritic community in the summer of 1932. Station 1C (Passamaquoddy bay)

1932	May 30	June 20	July 30	Aug. 21	Sept. 23	1932	June 20	July 30
Type of haul. Net	Metre	Metre	Metre	Metre	Metre	Type of haul	½ metre Net	Pump
Depth	35-0	35-0	35-0	30-0	44-0	Depth	30-0	30-0
Volume (displacement) 20 min.	8.0	26.7	1.9	12.0	13.3	Number per minute	•	
Relative percentage	•	•	•	•	•	Number per cubic metre		•
Calanus finmarchicus	30.0	7.1	2.8	3.7		Calanus finmarchicus egg		
Pseudocalanus minutus	28.4	84.7	2.8	9.5	12.1	Calanus finmarchicus nauplius		160
Metridia longa	8.4					Calanus finmarchicus copepodite	T	80
Balanus balanoides larva	8.4					Pseudocalanus minutus egg	2,847	760
Tortanus discaudatus	6.6	1.5	39.4	22.8	6.4	Pseudocalanus minutus nauplius	4,745	1,067
Euphausiid egg	3.3		42.6	1.7	.7	Pseudocalanus minutus copepodite		147
Acartia clausi	T	4.2		33.1	17.1	Temora longicornis nauplius	2,373	21,693
Eurytemora herdmani		1.3	0.9	5.3	46.4	Temora longicornis copepodite		
Centropages typicus			T	5.1	15.7	Acartia clausi nauplius		79,413
Temora longicornis				2.9	1.4	Acartia clausi copepodite	2,303	1,987

longicornis nauplii formed 2,373 per minute in net hauls on June 20, and 21,693 per cubic metre in pump samples on July 30, although no adults were taken until mid-August of that year. Traces of *Acartia clausi* in late copepodite stages in late May several weeks before the adults were first observed (June 20) in 1932 affords another example.

The present data are not sufficient to indicate the extent of vertebrate propagation in Passamaquoddy bay, as both eggs and larvae usually appeared in very small numbers (table XXI). Battle's (1930) work in this area would suggest that, as in the bay of Fundy (Huntsman 1918, 1922), propagation by species with pelagic eggs is largely unsuccessful.

ZOOPLANKTON INTERCHANGE WITH THE OUTER QUODDY REGION

The extent of zooplankton interchange between Passamaquoddy bay and the Outer Quoddy region through the three passages (fig. 41) must necessarily be proportional to the amount of water replacement, and hydrographic results indicate that such replacement is very slow (Watson 1936). Apparently the nature of the mixing mechanism is such that water tends to be drawn into the passage at the surface and bottom and retraces its steps at a mid-depth after mixing. This

takes place at the two ends of the passage. The maximum volume of mixed water occupies the greater part of the passage and is slowly replaced. Furthermore, according to Watson (1936, p. 183), "It appears that a large fraction of the water which comes out of the passages on the ebb tide returns into them on the succeeding flood and that the residual outflow of mixed water over a complete tidal interval is quite small."

According with this hydrographic evidence, biological observations, which were inaugurated during the peak of neritic propagation in mid-summer (1931), indicated from the beginning the existence of some barrier obstructing, to a considerable degree, the passage of zooplankton to and from Passamaquoddy bay. The endemic Passamaquoddy population was found to be restricted largely to the bay and the inner part of the Western passage (table XXIII). Elsewhere even at the end of the ebb tide the population in the passage consisted almost entirely of an immigrant stock from the bay of Fundy. Herring stomach analyses also indicated neritic species to be the principal food in Passamaquoddy bay, and offshore species the sole food in specimens from the passage (Johnson 1934, Battle, Huntsman et al. 1936, p. 419).

Repeated observations in 1932 (table XXIV) yielded substantially the same results except that at times neritic forms in relatively small numbers were found more widespread in the Western passage, and somewhat more abundant throughout the two Letite passages. In the latter area, however, there was a marked decline in the passages upon leaving the bay, and little evidence of dispersal beyond the immediate vicinity of the outer entrances.

As most of the fresh water entering Passamaquoddy bay passes out through the Western passage (Watson 1936, p. 195), replacement must be most active there. In the following table showing a comparison of the population in Passamaquoddy bay, the inner part of the Western passage and the outer part, observations in 1931 have been selected because in that year the neritic stock was much larger than in 1932, and with the dominant endemic species, *Acartia clausi*, ranging from 95.0 to 98.1 per cent, the extent of dispersal into the passage should be well indicated. These two bay stations being rather shallow, metre net hauls were made only at the surface. Near the bottom in deeper parts of the bay the relative percentage of *A. clausi* was probably somewhat smaller.

It will be seen that in the outer part of the passage (fig. 40, sta. 4) after the tide had ebbed for two and one-half to three hours *A. clausi* was totally absent, the hauls both at the surface and lower levels consisting almost entirely of boreal offshore species and larval benthos. In the inner part of the passage approaching Passamaquoddy bay (sta. 2) neritic species appeared in greater abundance at the surface, but the highest values occurred near the end of the flood tide and not when the water in the upper layer would have been expected to be entering from the bay on the ebb. Even at this inner station the boreal stock amounted to more than 80 per cent in the subsurface zone on both phases of the tide.

It would therefore appear that the relatively slow replacement of water in the passages (Watson 1936, p. 183) forms an effective barrier to rapid transit of

plankton organisms and the contributions from Passamaquoddy bay must be negligible even in the Outer Quoddy region. It is possible that during the spring freshets interchange is much more rapid, but these probably result in no detectable difference in the character of the zooplankton, because they occur before there is appreciable local propagation of either neritic or boreal species, and at a time when immigrant juveniles of the gulf stock in the upper levels tend to keep out of the Quoddy region in circuiting the bay of Fundy (Watson 1936, p. 188).

Referring again to tables XXIII and XXIV it is seen that in the Western passage even the smaller zooplankton organisms show a distinct stratification in

TABLE XXIII. Composition of the zooplankton population at selected stations in the Western passage and Passamaquoddy bay on different phases of the tide. Relative percentages in metre net collections.

Location	Passamaquoddy Bay		Western Passage (inner part)				Western Passage (outer part)			
Station	1E	1B	Cummings Cove to Kendall's Head (st. 2)				Off Wilson Head (st. 4)			
Date, 1931	Aug. 13	Sept. 14	August 8				September 16			
Phase of Tide (hours)	5E	2½E	5E	½E	5½F	5F	3E	2½E	½F	½F
Depth of haul (metres)	0	0	0	33-44	0	37-40	0	25-35	0	25-30
Volume (settling) in cc. (20 min.)	256		26	28.5	14.5	14	156	87	356	320
Acartia clausi	98.1	95.0	22.6	T	78.2	.8				.4
Calanus finmarchicus	T			91.2	1.2	69.0	53.1	31.8	34.9	42.5
Calanus hyperboreas			.9	.4			T	T	T	T
Centropages typicus		T			2.3		7.9	15.5	4.2	7.1
Euchaeta norvegica				T		1.6				T
Eurytemora herdmani		.4	T		2.4					
Halithalestris croni							1.0	7.5	.5	
Metridia longa				1.3		1.6		T	T	T
Metridia lucens						7.2		3.5	1.0	5.3
Pseudocalanus minutus		T	.4		4.1	.8	17.4	34.1	8.4	17.3
Temora longicornis	.7	T	.8		1.2					T
Tortanus discaudatus	.7		T	.4	T	T		.3	.5	.4
Balanus crenatus larvae			.4		.6					
Evadne nordmanni		1.4			T					
Podon leuckarti		T	T		.6					T
Podon polyphemoides		2.1	T		T					
Diastylis sculpta	T			.4		.8				
Calliopius laeviusculus		T							.5	
Euthemisto compressa								T	.5	
Meganyctiphanes eggs			17.8	.9	7.6	.8	17.3	13.4	40.5	20.3
Meganyctiphanes larvae		T	.4		T			.3		T
Thysanoessa inermis								T	T	
Thysanoessa neglecta								T	T	
Crago septemspinosus larvae	.7	T		.4	T	4.8		T		T
Cancer sp. zoea	T		T	T	T	8.0	T	T	.5	.4
Hyas coarctatus zoea										.4
Phialidium languidum							1.0	1.7	2.8	2.2
Turris vesicaria										T
Stephanomia cara							1.0		5.6	2.6
Aurelia aurita eggs			36.1							
Aurelia aurita larvae			13.5							
Sagitta elegans				1.3		.8	T	.6	.5	.9
Sagitta maxima							T	T		
Autolytus longisetosis			T	T	T		T	T	T	T
Tomopteris catherina							T	T	T	
Clione limacina larvae			T		T			T		
Littorina litorea eggs				.8	T	1.6				
Mytilus edulis larvae			5.2	1.7	T	T				T
Enchelyopus cimbrius eggs		.7	1.7	1.3	1.2	1.6	.5	T		
Tautogolabrus adspersus eggs							T			

daylight collections though the water was rather well mixed at the time. In table XXIII, the neritic species *Acartia* formed 22.6 per cent at the surface and but a trace between 33 and 44 metres on August 8, 1931, at station 2 (ebb tide), while *Calanus,* absent entirely at the surface, amounted to 91.2 per cent at the latter level. Similar stratification is seen in the vertical range of *Centropages* at this station in 1932 (table XXIV). Vertical differences in concentration are not so easily demonstrable at station 4 off Wilson head in the outer part of the passage, because the zooplankton population consisted for the most part of but one ecological group. However in table XXIV it is seen that *Centropages* formed

81.4 per cent in an oblique haul of 109 cc. and only 35.2 per cent in a haul of 31 cc. taken simultaneously at the surface. Again, although the species are not given, definite stratification is indicated in the outer passage (Calder beach) in a haul made on the flood tide on July 27, 1933, (Battle, Huntsman, et al. 1936, table X). At this time large copepods were almost three times as abundant and small copepods five times as abundant at the surface as at five metres.

Stratification of planktonic animals in a homogeneous water mass would appear to be most readily explainable in the following manner: considering that the uniform distribution of temperature and salinity in such a mass must result from gradual eddy diffusion, animals without power of motion would also be expected to gradually become evenly distributed throughout the mass in a similar

TABLE XXIV. Composition of the zooplankton population at selected stations in the Western passage. Relative percentages in metre net collections

Western passage.....	Inner part (station 2)				Outer part (station 4)		
1932.....	Sept. 12		Sept. 13		Sept. 13		
Phase of tide (hrs.).....	5¼E	5¼E	5½F	5½F	Low water	4½F	4½F
Depth of haul (metres)...	0	30-0	0	39-0	30-0	0	39-0
Volume (displacement)... cc.	7	11	10	31	17	31	109
Calanus finmarchicus....		T		6.8	2.1	5.2	13.8
Centropages typicus.....	6.6	82.5	31.2	77.7	78.4	35.2	81.4
Acartia clausi.....	77.6	10.1	45.8	7.4	3.6	1.8	T
Eurytemora herdmani ...	3.7		3.6	1.9	1.1	0.3	
Temora longicornis.....	3.3	0.3	0.4	0.4			
Tortanus discaudatus....	0.4		T	1.5	0.8		
Evadne nordmanni.....	1.2		1.1				

manner. Although transported in various directions their average displacement would probably be so small that with any power of independent locomotion, however feeble, they might easily counteract this diffusion process and respond to the same factors controlling their movement in more stable areas. To maintain themselves at any favourable level it would only be necessary to travel vertically at a rate greater than the rate of vertical eddy diffusion. Zooplankton organisms in the region are capable of a diurnal migration frequently exceeding 50 metres and sometimes 100 metres (Clarke 1934a, p. 538; 1934b, p. 447), whereas, although actual figures are lacking, the vertical rate of diffusion in the sea can hardly amount to 50 metres in 12 hours.

The foregoing comments refer to a homogeneous water mass. As a matter of fact the water in the Western passage, although mixed, was usually found to be

not entirely homogeneous. Vertical temperature gradients up to and even exceeding 3°C. in 40 metres were found at times, particularly on the ebb tide. (On August 8, 1931, at the time of the ebb tide hauls listed in table XXIII, the following temperature and salinity values were obtained: Surface, 14.1°C., 30.66°/$_{oo}$; 10 metres, 11.11°C., 31.49°/$_{oo}$; 25 metres, 10.41°C., 31.53°/$_{oo}$; 40 metres, 10.84°C., 31.55°/$_{oo}$). Supplementing these repeated records of slight temperature and salinity gradients, the observed vertical stratification of euphausiid eggs (without power of locomotion) in violently turbulent water would appear indicative of rather limited vertical displacement as compared with lateral eddy movement. Animals could hardly be transported passively to the surface by mechanical mixing in water exhibiting even slight thermal stratification. Violent vertical mixing may take place in whirlpools on certain phases of the tide, and at such times animals may be distributed through the mass, but these are local phenomena and the zooplankton appears to quickly stratify out again. Eggs of *Meganyctiphanes norvegica* at station 4 on September 16 (table XXIII) were twice as abundant in a haul of 356 cc. at the surface as in a haul of approximately similar volume (320 cc.) at 25-30 metres. The percentage difference was also great between the surface and lower levels at station 2 on August 8 both during the flood and ebb tide, as seen in the same table. Similar vertical differences were also observed at station 2 on September 16 (15% at surface, 4.6% at 36-40 metres) and station 4 on September 15, 1931.

In light of the foregoing observations there would seem to be little doubt that the swarms of actively swimming euphausiids, commonly observed during the summer at the surface in the Western Quoddy passage and less frequently in other turbulent areas like Frenchmans bay (Dahlgren 1925) and the outer part of the bay of Fundy (S. I. Smith 1879, p. 90; Moore 1898, p. 401), are not passively transported from the lower levels. On one occasion while a hydrographic station was being made between Eastport and Welchpool (station B. W., fig. 21, Watson 1936) on August 7 some of the largest local swarms observed in 1932 appeared at the surface with the water stratified to the extent indicated in the following table:

Depth (metres)	Density	Salinity (°/$_{oo}$)	Temperature (°C.)
0	24.65	32.09	10.30
5	24.72	32.09	9.88
10	24.79	32.12	9.65
20	24.82	32.16	9.60

Why then do euphausiids appear at the surface by day in this locality? With so little positive evidence it is dangerous to hazard a guess. The abundance of eggs (table XIX, sta. M1 and M5) indicates that *Meganyctiphanes norvegica,* the species most commonly reported, is generally distributed along the New Brunswick coast in summer and might be expected to enter the passage at any time. That the concentrations observed at the surface represent sporadic invasions of short duration and not a resident population is suggested by the fact that in both

1931 and 1932 attempts to obtain material one or two days after swarms had been reported repeatedly proved unsuccessful. On such occasions none were found at the surface and at best only occasional specimens in the lower levels. Again the fact that our surface collections of *Meganyctiphanes* concentrations have consisted entirely of large mature adults, although juveniles of 12 to 18 mm. dominated the population in the region at the time (p. 313), would also suggest a swarm of one size group. This might be considered indicative of a spawning migration were it not that at times the swarms in late summer were found to contain a considerable number of *Thysanoessa* which terminates its spawning season everywhere in the region before the end of June. In one such collection taken by Dr. A. H. Leim at the surface in the Western passage on August 31, 1933, three species of *Thysanoessa* outnumbered *Meganyctiphanes* 295 to 35. Yet all records at hand occur in the period between March and September (Bigelow 1926, p. 150), which coincides with the spring and summer spawning period of the latter species. Thus on the basis of this apparent short sojourn of individual concentrations (although invasions may be of frequent occurrence particularly in August and September) of one age group (individuals 28-31 mm. exceeding 87% in the case of *Meganyctiphanes*), it may be suggested that migrant swarms entering the passage find the turbulent water unfavourable and, disregarding their usual day levels, swim about actively in an effort to escape to the more stable conditions to which they are accustomed. Were euphausiids present continuously in such numbers in the passage during the summer months, they should appear more regularly in net hauls than the records indicate (table XXIII).

DISCUSSION

In the foregoing chapters an attempt has been made to analyze the composition of the zooplankton population in the region, quantitative and qualitative seasonal changes, and those physical environmental conditions considered to have the most readily detectable influence on its production and geographical distribution.

Composition of the Population

The dominance of Crustacea in the animal plankton is clearly indicated in all available data from the gulf and bay of Fundy. As shown in the following table (XXV), even during the period of greatest propagation of other invertebrates, from April to September in 1932, crustacean averages for the region ranged from 87.2 to 97.6 per cent. Copepods usually comprise the bulk of the stock (numerically) except in some localities in the immediate vicinity of the coast during the barnacle breeding season (April-May), and in very limited areas when swarms of other Crustacea (euphausiids, Cladocera, and less commonly amphipods), Sagittae, Medusae, molluscan larvae and rotifers occur. Such swarms are usually of rather short duration and exert little influence on averages for the region as a whole.

Another important characteristic is the remarkable uniformity of the population in the open gulf at all times, consisting largely of boreal endemic species. In inland waters there is the addition of and sometimes to a large extent replace-

ment by neritic forms and larvae of benthonic invertebrates in spring and summer, but their range of appreciable influence rarely extends far offshore. Eggs and larvae of but a few species of vertebrates are found in very large numbers and then only for comparatively short periods, as rapid dispersal from offshore spawning areas quickly dilutes the stock. The two remaining ecological groups represented in the region, northern and southern migrants, are chiefly of interest as indicators of inflow into the gulf.

TABLE XXV. Relative percentages of copepods and other Crustacea

1932	TOTAL AREA			GULF OF MAINE Western area		
Month	% copepods	% other crustacea	total crustacea	% copepods	% other crustacea	total crustacea
April	45.3	41.9	87.2	52.8	35.6	88.4
May	77.2	15.2	92.4	84.0	9.2	93.2
June	85.5	11.7	97.2	82.5	15.4	97.9
Aug.	72.4	18.1	90.5	68.2	22.1	90.3
Sept.	96.9	.7	97.6	99.5	T	99.5

Although some 30 members of the dominant boreal group are common to the region, the population throughout the year is composed largely of a very few species. But six forms, shown in the following table (XXVI), averaged more than one per cent, and these in all observed offshore areas of the gulf and bay of Fundy totalled more than 83 per cent.

TABLE XXVI. Relative percentages of the six dominant boreal endemic forms. Average values within the

	Bay of Fundy				April - September	
	Year	Year	August-Sept.		Western	Central
	1917	1931-32	1931	1932	area	area
Calanus finmarchicus	80.7	38.6	49.1	35.6	45.3	49.1
Centropages typicus	.1	22.6	7.4	26.0	8.2	3.2
Pseudocalanus minutus	8.1	10.0	3.9	4.2	3.9	6.2
Metridia lucens	1.3	7.1	2.3	10.0	19.4	15.6
Euphausiid eggs	2.7	8.9	28.6	8.7	11.6	10.9
Sagitta elegans	2.6	2.2	2.2	1.6	.4	.5
Total %	95.5	89.4	93.5	86.1	88.8	85.5

BIOLOGY OF THE ZOOPLANKTON POPULATION

ANNUAL CYCLE

In so nearly a closed system as the gulf, quantitative fluctuations in the zooplankton are indicative of periods of local augmentation and depletion. The population is at a minimum in late winter and early spring. In the case of such typically boreal copepods as *Calanus, Pseudocalanus, Oithona* and *Microstella,* the winter stock consists of late copepodites which mature and spawn with the warming of the water in early spring. Beginning in March or early April there is a series of three or four generations, each ranging from six weeks to two and one-half months, until September. Thereafter the stock remains in late developmental stages to form the winter population.

In *Centropages typicus,* showing both neritic and open gulf characteristics, there is some indication that there may be a winter egg as the species is sparse or absent for much of the year. Larvae in 1932 appeared as early as June but did not become abundant until August. There is one brood in the eastern gulf and possibly two in that portion of the population originating west of Mount Desert, but this has not been definitely established. The stock reaches its peak in September and declines during the early winter (fig. 43).

in the zooplankton population in 1932. Metre net collections

Central area			BAY OF FUNDY		
% copepods	% other crustacea	total crustacea	% copepods	% other crustacea	total crustacea
28.5	66.7	95.2	54.5	23.5	77.9
74.5	18.9	93.4	73.1	17.4	90.5
85.3	12.2	97.5	88.7	7.4	96.1
83.3	8.9	92.7	65.3	23.4	88.7
100.0	0	100.0	91.2	2.3	93.5

Neritic copepods are summer spawners in this region and for the most part have a winter resting stage. The more common species, *Acartia, Tortanus,* and *Temora* in Passamaquoddy bay, appear to pass through two generations before declining in the autumn.

In the higher Crustacea there is but one annual brood. The most common

calculated from the total zooplankton population in metre net collections from all stations designated areas

1932		May 1932			September 1932		
Offshore gulf	Bay of Fundy	Off Cape Ann	Eastern channel	Brown's bank	Outer gulf	West coast Nova Scotia	Georges bank
49.5	39.3	74.9	91.0	46.6	28.3	62.6	1.8
.2	10.4	1.1			.3	13.7	88.8
1.6	16.0	11.8	1.0	47.2		11.4	.3
30.8	6.9	9.8	4.0		32.6	T	1.8
7.9	7.0	.3			.1		
.2	4.3	T	T	1.6	T	3.1	2.6
90.2	83.9	97.9	96.0	95.4	61.3	90.8	95.3

euphausiids, *Meganyctiphanes* and *Thysanoessa,* like the copepods, pass the winter in late juvenile (cyrtopia) stages and mature with rising spring temperatures.

In most of the non-crustacean species there is also indication of but one generation each year, but one at least, *Sagitta elegans,* has been shown to have several (Russell 1932, p. 141). Our data have not yet been fully analyzed, but the repeated maxima of eggs and different size groups during the summer suggest an annual cycle in the region somewhat comparable to that of boreal copepods. The propagation period would appear to be longer than that of copepods however, since well advanced young (11-15 mm.) were found in the gulf in late April in 1932, and eggs in the bay of Fundy on October 2 in 1917 (Huntsman and Reid 1921, p. 107).

Adults of most planktonic animals apparently die off soon after spawning, the males preceding the females in the case of *Calanus*. This results in a replacement of the stock with each generation. Euphausiids may form an exception, for, although largely replaced each year, a part of the population in the bay of Fundy appears to survive a second year (no evidence was found to indicate that the euphausiid stock in the gulf is not wholly replaced each year). Old adults of 28 to 35 mm. were present in the bay in November 1931 when the largest members of the earliest spring crop (April) had not yet attained a length of 24 mm.

FIGURE 43. Distribution of *Centropages typicus* in September, 1932. Relative percentages in metre net collections.

BREEDING STOCKS

Being closely correlated with temperature, the delay in vernal warming to the eastward in the inner gulf is reflected in the breeding periods. Earliest propagation appears to take place in the outer gulf, followed by the western coastal zone and thence eastward to the bay of Fundy. The New Brunswick side of the bay is the last to respond, due to the influence of the Saint John outwash (Watson 1936, p. 188). There is an average difference of about one month in the time of spawning of observed boreal species in each of these three general areas, beginning

in the outer gulf in early March, the western area in early April and the eastern gulf, including the bay of Fundy, in May or later.

On the basis of this regional variation in the time of spawning, it is possible to distinguish different breeding stocks. "These stocks are not permanently restricted to their respective localities, but merely represent delayed maturation of that portion of the winter population . . . . . which happens to be located in the eastern part of the gulf and bay of Fundy during the spring, and earlier maturation in areas to the westward where the water mass responds more rapidly to vernal warming" (Fish 1936b, p. 197). However, with the annual cycle starting at significantly different times, and with approximately the same interval of development, the distinct breeding periods are continued in subsequent generations that year, no matter where the young are dispersed, any acceleration of growth in members of the eastern stock transported into the warmer western area being of minor degree.

A possible explanation of the ripening of the gonads of the outer gulf and western breeding stocks almost coincident with or even preceding vernal warming of the upper strata, may be found in the inflow of warm bottom water which maintains uniform temperatures of 5 to 6°C. in the basin of the gulf throughout the winter (p. 195). In areas not so affected, sexual development of even two year old euphausiids is much slower.

PRODUCTION AREAS

The vernal crop (March-April) of boreal species appears to be derived largely from adults maturing in the western or outer gulf. In some, like *Calanus finmarchicus* (Fish 1936a) and *Meganyctiphanes,* where an offshore brood was not detectable, the western coastal area may form the principal source of the population in the region. In others, like *Pseudocalanus* and *Oithona similis,* the bulk of the stock following the first brood appears to be derived from the outer gulf and eastern basin (Fish 1936b and c). A barren spring and abundant summer plankton was also observed by Bigelow (1926 p. 89) in the eastern basin (see p. 223).

Two distinct populations of *Centropages typicus* were found in 1932. One was confined to the inner gulf and bay of Fundy. The other occurred over Georges bank where it formed up to 92 per cent of the zooplankton in mid-September. Although abundant at all stations on the bank, none were taken in the basin of the gulf or in the drift to the coast.

The source of *Metridia lucens* remains problematical, for although ranking fifth (7.1%) in the bay of Fundy zooplankton in 1931-1932, and second (17.5%) in the gulf during the period April-September (1932), eggs and early larvae were entirely absent in all collections. (But three specimens of unidentified nauplii representing two species were taken during the period of the investigation). In its general distribution in the western Atlantic and relative abundance in the gulf, it shows the characteristics of a typical boreal form. However, in Bigelow's records covering a period of years there was no evidence of concentrations indicative of local centres of reproduction and "the fact that it has been found most

regularly in the eastern and southern parts of the gulf points to a certain amount of immigration via the two channels and across Browns bank from the continental shelf off Nova Scotia" (1926, p. 262). His chart of centres of abundance during the year (p. 257) also suggests a winter population in offshore waters, with a movement into the eastern coastal area following vernal augmentation. These records, combined with the fact that appreciable propagation could hardly take place anywhere within the gulf and not be indicated in collections covering the spring and summer period, justify a tentative conclusion that the *Metridia lucens* population consists largely if not entirely of immigrants from outside waters. An important propagation area must be located near the entrance to the gulf, however, because young reach the inner coastal region in fourth and fifth copepodite stages. The following relative percentages of copepodites to adults occurred in the general region in 1932: April 36.7, May 81.4, June 58.4, August 77.8, and September 70.6

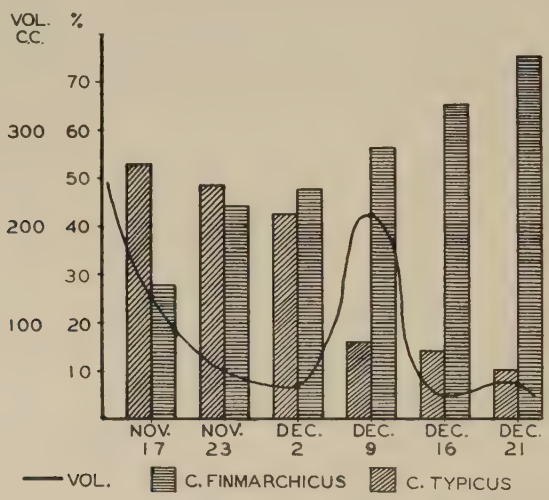

FIGURE 44. Showing decline of *Centropages typicus* stock in 1931.

per cent. The rise in copepodite values in May and August may represent successive broods of migrants. Augmentation by juveniles on these occasions was particularly evident in the Quoddy region (sta. 5). Here on March 5 and April 15 the hauls yielded only adults. An influx of copepodites, amounting to 60 per cent of the *Metridia* stock on the nineteenth, occurred in May. Small numbers of adults only were found on June 20 and July 30, but in August copepodites again appeared and rose to 66 per cent by September 26.

A comparison of the quantitative distribution of adults (figs. 15 and 16) and larvae (Fish 1936a, 1936b and c) of boreal endemic species with summer temperatures (figs. 6 to 9) shows a close correlation. Localities sparse in all stages coincide with the range of minimum surface temperatures. Previous evidence of unsuccessful development at low temperatures has been found in *Enchelyopus cimbrius* in Passamaquoddy bay (Battle 1930), and in *Sagitta elegans* (Huntsman and Reid 1921, p. 110), *Calanus finmarchicus* (Miss N. E. Wright in Cowie 1929)

and fishes having pelagic eggs (Huntsman 1918, p. 65) in the bay of Fundy. Miss Wright's statement that the surviving *Calanus* stock enters the bay of Fundy in copepodite stages agrees with present results, but the basis for her conclusion, i.e. almost complete absence of early stages, seems erroneous. Eggs (up to 19,444 per min.) and nauplii were widespread and often in comparatively large numbers in the bay during the propagation period both in 1931 and 1932 (Fish 1936a).

However, in the western gulf adults of the boreal plankton population occur regularly at night at the surface at temperatures of 19°C. or more, and larvae by day at depths of 25 to 50 metres at temperatures ranging as low as 8°C. (Gran and Braarud 1935, fig. 296). Euphausiid larvae, for example, in cyrtopian stages in August were found in greatest abundance during the daylight hours at temperatures below 8°C. off Casco bay, but not in the bay of Fundy where the surface water averaged from 12 to 14°C. at the time. It is therefore evident that other factors must also be taken into consideration.

Whereas a combination of two factors, light and turbulence, apparently serves to restrict diatom production in the bay of Fundy (Gran and Braarud 1935, p. 280), it has been suggested that turbulence and temperature account for the lack of successful propagation and the small population of boreal zooplankton (Huntsman 1918; Fish 1935) in the coastal zone eastward from Mount Desert (including the bay of Fundy). "The observed descent of larvae to levels of relatively low temperature by day and the rise of adults to warm surface waters at night indicate that all can apparently survive the most extreme conditions existing in the region provided that there can be periodic access to water within the required thermal range." (Fish 1935, p. 98). In turbulent areas like the bay of Fundy and eastern coastal portion of the gulf where throughout the summer one finds neither warm surface nor cold bottom water, environmental conditions would not appear to be favourable either for adults or young.

The influence of these two factors is also seen in the records from inland waters. In Frenchmans bay in 1930, with low bottom (6.9 to 10°C.) and surface (12 to 15°C.) temperatures (July-September), the latter resulting from moderate tidal mixing in the upper levels, a comparatively abundant stock of boreal adults adjacent to the bottom was apparently not affected, but larvae were even sparser than in the bay of Fundy (see p. 288). Eggs of *Meganyctiphanes* and *Tautogolabrus* (M. P. Fish 1931) were at times particularly numerous, but surface temperatures apparently remained too low for successful incubation. Farther west in the relatively stable waters of Casco bay with low bottom and high surface temperatures, both adults and young thrive (euphausiid larvae amounted to 40.6% at sta. A in August 1932, table XIX). In the relatively homogeneous water of Passamaquoddy bay the scarcity of both boreal adults and larvae throughout the summers of 1931 and 1932 indicates conditions somewhat comparable with the bay of Fundy.

It therefore seems evident that although mechanical mixing does not in itself appear to be a limiting factor, as an agent in affecting temperature distribution

during the period that the water mass is subjected to solar heating, it marks the boundaries of biological barriers. Summer surface temperatures, as indicative of the degree of turbulence, can be considered to define directly areas most favourable for production of boreal species in the region, and indirectly and in a more general manner the quantitative distribution of the adult zooplankton population. The extent of mixing in different localities is shown in the following table.

TABLE XXVII. Maximum vertical range of temperature at representative stations

1932.....	Gulf of Maine				Bay of Fundy			
Station.....	26	29	31	32	5	8A	11A	36
April.....	3.3°C	0.9°C	1.6°C	0.4°C	0.5°C	0.3°C	0.7°C	1.2°C
May.....	5.3	3.6	1.8	0.8	0.7	0.2	0.3	3.3
June.....	10.7	4.9	5.0	0.9	1.0	1.6	0.3	3.6
August.....	13.7	10.3	10.4	1.5	2.5	3.6	4.1	6.0
September.....					2.2	0.5	0.8	2.2

The cold Nova Scotian current (Bigelow 1927, p. 832) may extend the boundaries of the unproductive zone (p. 311) for a time in the spring by retarding surface warming over a large part of the eastern basin during the period of vernal propagation. Its influence is temporary, however, and later, as previously described (p. 309), extensive propagation takes place in this area, particularly of species in which the numbers of larvae do not reach their seasonal peak in the first brood (*Pseudocalanus* and *Oithona*).

Unlike boreal zooplankton and fishes having pelagic eggs, benthonic invertebrates in all stages have a relatively wide thermal range and appear to suffer little from the results of turbulence. In fact larval pelecypods (*Mytilus* and mollusc DE, p. 227) were found in the largest numbers where most violent mechanical mixing occurs. (Rotifers too were concentrated in the same manner both in Frenchmans bay and the Fundy region (p. 244)).

Were it possible to assign a definite thermal range for the boreal group, or even individual ranges for each species, the problem of establishing definite areas as productive or non-productive would be simplified. This is not possible, however, either in the case of adults or developmental stages.

In adults the existence of physiological races with different thermal ranges is well recognized, and their presence in western Atlantic waters evident. The maximum temperature limit of boreal species like *Calanus* in the bay of Fundy is significantly lower than at Woods Hole. (This species has also been taken at the surface in the Florida straits in July (Field and Fish 1929, p. 2)). Therefore until the geographical ranges of the different races along the Atlantic coast have been determined, it will be difficult to correlate results from different regions. Although it has not been established we are assuming that, in each species, but one race exists in the gulf of Maine and bay of Fundy.

Within the gulf-Fundy region, however, developmental stages offer a further problem. In order to explain the varying degree of success in survival of eggs and larvae in different parts of the gulf and bay, it seems necessary to assume that the lethal temperature limits vary in different stages of development. It has been observed in both marine invertebrates and vertebrates (Vernon 1899, Huntsman and Sparks 1924, Runnström 1927, Bogorov 1932, etc.) that certain species in their earliest and adult stages tend to be more stenothermic than in intermediate stages. In Runnström's experiments *Cione* larvae survived normally at a temperature 10°C. higher than when hatched, and Vernon found that the lethal point in *Strongylocentrotus* was 11.8° higher than for eggs. This permits an immigrant stock entering in larval stages to survive in certain localities where successful breeding cannot take place.

The situation in the case of some true planktonic species appears to be different. Here observational data indicate that early and late stages are relatively eurythermic and intermediate larval stages more stenothermic. There is a fair percentage of survival of late copepodite stages of copepods entering the barren turbulent region, which mature and spawn. These eggs are fertilized and pass through varying intervals of incubation. Some hatch but the larvae soon disappear. Larvae surviving in more favourable areas appear to become increasingly stenothermic as development progresses. In the vernal crop, although eggs are hatched in temperatures of 7°C. or less in April, larvae (nauplii and early copepodites of copepods; calyptopis and furcilia stages of euphausiids) apparently do not survive at similar temperatures when transported into the turbulent area in May and June. In the case of *Meganyctiphanes norvegica* in 1932, calyptopis and furcilia stages were found restricted largely to the western area where surface temperatures at this time ranged from 10.5 to 15.9°C. Again in August early cyrtopian stages (9 to 11 mm.) were found for the most part restricted to the western area in surface temperatures ranging from 14 to 19.3°C., the greater number occurring where the temperature exceeded 15°C., although the surface temperature throughout the bay of Fundy (except in the Quoddy region) was 5 to 6° higher (12°) than that at which they hatched.

The development of boreal forms would thus appear to be closely attuned to normal vernal warming of the surface water, and most favourable conditions for survival occur in stable areas where each progressive stage (until maximum summer temperatures are reached) is subjected to an increasingly higher surface temperature. Approaching the adult stage the young appear to again become increasingly eurythermic, as indicated by a wide distribution of the more advanced members of the spring crop of *Meganyctiphanes* (12 to 18 mm.) in August, and the influx and apparent survival of members of the summer crop at similar stages in the bay in November and December.

Variable resistance in developmental stages was not as readily detectable in copepods, but in general conditions appear to be similar, as only those entering the turbulent area in copepodite stages survive. It is in these stages that the winter population of the bay of Fundy is recruited.

DISPERSAL

Dispersal of eggs and larvae, concentrated in the upper levels, corresponds closely with non-tidal circulation (Bigelow 1926, pp. 70-75 and 155; Fish 1936a, 1936b and c). Movements of both the western and eastern breeding stocks, when occurring in sufficient numbers, were found to be reasonably well indicated by monthly changes in the distribution of larvae in progressive stages of development.

Following vernal propagation in the western coastal area, larvae of the dominant species, *Calanus finmarchicus,* were found extending offshore and eastward around the outer margin of the gulf (Fish 1936a, fig. 6A). An appreciable part of these migrants or their progeny were found, on subsequent cruises, completing the circuit within the gulf or entering the bay of Fundy along the Nova Scotian coast as described on p. 205. Later, as some species become established in the eastern basin, summer broods (p. 312) are then supplemented by important contributions from this area, at which time the number of early stages entering the barren zone is greatly increased. These however, like locally produced larvae in the bay, soon disappear.

The dispersal of developmental stages was reflected in a general way in the distribution of late juveniles and adults, but the movements of the latter appear to be somewhat slower because, in descending during the day, they encounter a slower rate of subsurface drift. However, it is evident from the distribution of eggs and early larvae (Fish 1936b, figs. 6A and B; 1936c, fig. 6B) that a considerable number of adults subjected to low temperature and delayed maturation (eastern stock) are transported west of Mount Desert before spawning. In fact it is possible that the maintenance of the eastern stock is to a large extent dependent on these migrant adults reaching the proximity of favourable areas before spawning, as the vernal brood in May appears at a time when even the eastern basin appears unproductive (p. 312).

Since the various areas form sectors in a cyclonic system and are subjected to a continuous non-tidal drift, there arises the question of how the western area retains such a large concentration of zooplankton animals in all stages of development, and also how turbulent areas remain so consistently barren.

With regard to the former, during the propagation period it would be reasonable to suppose that eggs and larvae of the local crop would be transported seaward out of the region, and, with a relatively unproductive zone to the eastward available as a source of supply, the coastal zone would tend to be largely depleted of larvae. As this does not occur other factors must serve to counteract offshore dispersal of a substantial part of the stock. No conclusive explanation is afforded by the present data, but the distribution of larval stages of *Calanus finmarchicus* of the first western brood in a section off Casco bay on May 2, 1932, is suggestive. As one would expect, extending seaward from station 25A (fig. 2) progressively later stages were found along the course of the off-shore drift. In figure 45, nauplius stages I-II and III-IV are seen to be equally abundant at

station 25A. At station 24A (10 miles seaward) stages III-IV dominated, at station 23A (10 miles) stages V-VI, and at station 26 (20 miles) many were still in nauplius stage VI but these were far outnumbered by combined copepodite stages I and II. At this point there occurred an apparent reversal of course with

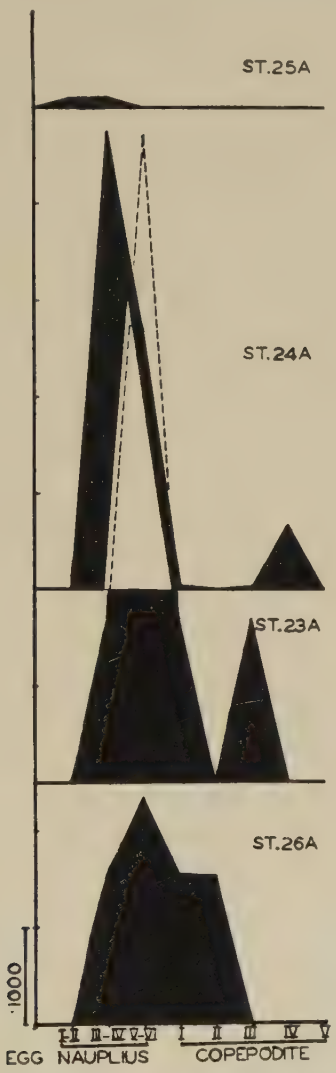

FIGURE 45. Distribution of *Calanus finmarchicus* larvae in different stages of development in a section off Casco bay in April, 1932. Oblique haul, 50 metres to surface; number per minute of towing a half-metre net.

a subsequent progression of copepodite stages in a shoreward direction, copepodite III dominating at station 23A, and copepodite IV at station 24A. Considering the almost complete absence of intermediate stages at stations 23A and 24A it would appear that, having reached the second copepodite stage in the region of

station 26, the larvae then retraced their steps. Such a procedure would be inconceivable at the surface, but, if a counter movement toward the coast takes place in lower levels, older stages descending to greater depths would tend to be carried with it. Our hydrographic data are insufficient to afford much assistance but they offer no negative evidence. If a compensating subsurface movement is found to occur it may prove of considerable importance in maintaining the stock in the western area.

The reason for the consistently small summer population in the turbulent areas is more obvious, for, added to unsuccessful local propagation, there is an effective physical barrier retarding the rate of interchange with the more productive neighbouring areas, comparable with that in the Quoddy passages (p. 302). As stated by Watson (1936, pp. 190-191) ". . . any area which contains homogeneous water, however this may be formed, will be conspicuously lacking in permanent residual currents." Thus contributions from outside waters must at best be acquired relatively slowly. Supplementing present plankton data there is the evidence afforded by drift bottles (pp. 209-213) and previous observations (Bigelow 1914a, p. 34, p. 130; 1926, p. 83). During the winter months, when the population is dominated by long lived copepodite stages of copepods (Fish 1936a, p. 137), volumes may gradually become more comparable with other areas, but following vernal augmentation these forms quickly die off, and as copepodites of subsequent broods are introduced, they mature and disappear so rapidly that no appreciable accumulation appears to take place, at least until the winter stock again becomes established.

NATURAL ECONOMY

The extreme seasonal fluctuations in the volume of both adult and larval zooplankton organisms must be of vital importance in the natural economy of the region. (The present method of numerical analysis does not show in true proportion the relative importance of euphausiids. Although usually far outnumbered by smaller species, they frequently form the bulk of the catch (p. 239). As described on page 219, plankton volumes are at a minimum in early spring (late February and early March) and rapidly increase to a peak in May-June following vernal propagation when the new crop approaches adult size (figs. 20 and 21). Almost all of the dominant boreal species begin spawning in late March or early April and all make contributions, but the quantitative fluctuations in the mass reflect to a large extent changes in the stock of the most important species, *Calanus finmarchicus* (Fish 1936a, p. 121). Accordingly, with the rapid depletion of the *Calanus* stock during the critical period of maturation (between the maximum of copepodite stages of the first brood in late May and the maximum of eggs of the second in June, (Fish 1936a, p. 136) there occurred the decline in total zooplankton volume indicated in figures 20 and 21.

Whether the longer lived (winter) parent stock of the first brood is more prolific, or whether the coincident increase in predatory enemies of the larvae is accountable for the continuous decline in volume after the May peak, is not known,

but the decline continued throughout the remainder of the summer in spite of subsequent broods with much larger parent stocks than were present in March. Assuming that the two years are comparable, the difference of 80 per cent (p. 216) in the September and April volumes represents the degree of unexpected winter depletion in the region.

The importance of larval stages of pelagic crustaceans cannot be too strongly emphasized, because of their value as food for larger invertebrates and vertebrate larvae. As has been pointed out in previous papers (Fish 1936b, p. 214; 1936c, p. 185), the relative numerical value of larvae of the various species is not necessarily the same as that of the adults. Based on the comparative abundance of individuals in developmental stages and the rate of depletion, *Pseudocalanus* and *Oithona* are at times of far greater importance to animals feeding on copepod larvae, than *Calanus*. Ogilvie (1927) also found *Pseudocalanus* and *Oithona* to be the most abundant food in the stomachs of post-larval herring from the Scottish coast.

Another factor of importance in the economy of the gulf and bay is the occurrence of the seasonal maxima of different dominant species at successively later periods during the summer. This results in an abundant supply of copepod larvae widespread in the region from April until September. Whereas *Calanus* reaches its peak in May (first brood), *Pseudocalanus* is most abundant in June (second brood), and *Oithona* (third brood) in August. Later in August *Centropages* appears and forms an important part of the larval stock in September. Why with all of these important boreal species, with the exception of *Centropages*, passing through a similar progression of generations, one should have the first brood of larvae dominant, another the second, and still another the third, is difficult to explain, but there results a rich source of food throughout the propagation period of summer spawning fishes.

TABLE XXVIII. Mean numbers of larval stages of dominant species of copepods in the total region in 1932. April-June: number per minute. August-September: number per cubic metre.

1932	Calanus finmarchicus	Pseudocalanus minutus	Oithona similis
April	2,007	7,126	1,112
May	7,024	11,484	5,918
June	2,156	21,303	8,919
August	977	5,639	34,852
September	41	3,506	3,262
Apr.-Sept. (Mean)	2,441	9,812	10,813

Very early pelagic larvae of *Ammodytes, Clupea, Gadus* and *Pholis* observed in the present investigation were found to be feeding almost exclusively on crustacean larvae. Unfortunately the numbers obtained were not sufficiently

large to be conclusive, but if they prove representative, a correlation may be found to exist between fluctuations in year classes of some of the spring and summer breeding fishes, and quantitative variations in their food. In the case of cod, the breeding season north of cape Ann (Bigelow and Welsh 1925, p. 422) coincides with vernal augmentation of *Calanus* and *Pseudocalanus*. Farther east on the Grand bank, young of the two groups were also observed together on June 5 to 17, 1924, by the senior author, and stomach contents of 17 early larval cod examined consisted entirely of *Calanus* nauplii. (Two specimens at station M5 (46° 48'N., 51° 45'W.) on June 13, and 15 specimens at station M8 (46° 44'N., 52° 25'W.) on June 17, 1924, in vertical hauls from 100 metres). It seems conceivable that if for some reason the seasons should not coincide and cod hatched before copepod propagation began or after development had reached copepodite stages, accessible food might be sufficient for only a small part of the usual stock. Although there is no actual proof that this ever occurs in the region, the possibility is suggested by the observed annual variation both in the size of copepod stocks (*Centropages,* pp. 236-237) and the time of spawning (*Acartia,* p. 294).

Larval crustaceans also frequently form an important source of food for adults of such ordinarily selective feeders as mackerel, as has often been noted. A number of this species in an open pool at Woods Hole in 1933 were observed by Mr. O. E. Sette to have two distinct types of feeding: (1) the selection of relatively large particles of food (chopped fish or molluscks); and (2) the indiscriminate straining of water for more minute organisms.

The regional distribution of food available for plankton feeders parallels closely relative productivity in different areas. It has been seen (pp. 219 to 227) that the supply in the gulf is much greater than that of the bay, the largest volumes occurring in the productive western and outer gulf during the early season and later expanding to include the eastern basin in midsummer. Within the bay of Fundy, which depends largely on immigration for its zooplankton supply, the largest volumes, most closely approximating those of the gulf, are found along the Nova Scotian shore in the entering drift.

According with previous records (Bigelow 1914a, pp. 34, 104 and 130; 1926, pp. 83-85) the supply, both in 1931 and 1932 (pp. 220 and 294) was consistently sparse in the non-productive coastal zone eastward from Mount Desert, with minimum amounts usually centred in and about the Quoddy area (figs. 41 and 42). Furthermore, as shown in figure 42, within Passamaquoddy bay the quantity of zooplankton throughout the year was generally even scantier than in Outer Quoddy waters (sta. 5). It would thus appear that so far as total abundance of this type of food is concerned the Quoddy area forms the least favourable of all observed localities in the entire region.

This point is of importance in the problem confronting the Commission because the possibility that the reported concentrations of sardine-sized herring in the Quoddy region are correlated with the zooplankton food supply has repeatedly been advanced (Graham 1936, pp. 122-125). For such a correlation there must

either be an abundance of food, or it must be particularly accessible. That correlation of herring and its food in Quoddy waters is not possible in terms of local production, or the local amount of food, has also been concluded by other recent observers (Battle, Huntsman et al. 1936, p. 427).

Again the possibility suggested by Huntsman (1934) that, although smaller in volume, the plankton distributed through the water mass in the mechanical mixing process is rendered more accessible to herring feeding in the upper levels during the daylight hours (Battle 1934) than a larger zooplankton population concentrated at or adjacent to the bottom, seems equally open to question in light of present data indicating that vertical stratification of even the smaller zooplankton organisms does not generally appear to be seriously affected over most of the western passage even during the periods of most violent turbulence. To other examples (pp. 302-304) showing the character of the mechanical mixing in this locality to be such that vertical movement is rather limited as compared with lateral eddy displacement, may be added the following: (1931) station 3, September 16, *Centropages typicus* 28.1 per cent at the surface, 7.8 per cent at 25 to 30 metres, and *Pseudocalanus minutus* 18.5 per cent at the surface, 30.7 per cent at 25 to 30 metres; station 4, September 15, *P. minutus* 8.1 per cent at the surface, 21.8 per cent at 25 metres. Vertical stratification of plankton is also implied in a recent statement on the feeding of herring by other observers, "The fact that they feed near or at the surface in the Quoddy passages during the day is not owing to there being more food near the surface, for the reverse is the fact . . ." (Battle, Huntsman, et al. 1936, p. 421).

It seems unlikely that euphausiids, the one form commonly observed swarming by day in the upper levels, could alone account for a sardine-sized herring concentration in the Quoddy region, for in addition to their apparent sporadic occurrence in appreciable numbers (p. 304), stomach analyses show no evidence that they are especially sought after as food. The food taken appears to be that most readily available in the locality at the time, although some variation with the size of the fish has been noted (Johnson 1933), the percentage of smaller plankton forms (*Pseudocalanus*) being somewhat greater in herring of small size (13 to 15 cm.). Thus in comparing 1931 summer net collections (table XIX) with stomach analyses in 1933 (Johnson 1933) it may be seen that dominant members of the population at that season, *Calanus, Pseudocalanus, Eurytemora, Temora* and *Acartia,* also, occurred most often in herring. Within Passamaquoddy bay (apparently before the *Acartia* maximum in 1933) the neritic copepods *Eurytemora* and *Temora* dominated in stomach samples, while in the passages the boreal species, *Calanus, Pseudocalanus* and *Meganyctiphanes,* formed almost the sole food. Throughout the whole Quoddy region Johnson found copepods the most common food. Similar results have been obtained in controlled feeding experiments. "Overnight, with the light kept on, the copepods all disappeared, but there was no indication that the fish had taken any of the Euphausiids introduced, which they cannot capture so readily." "Moreover, experiments in 1934 showed that

the herring will take dead *Meganyctiphanes* only when chopped in pieces." (Battle, Huntsman et al. 1936, pp. 410 and 412).

The whole question of accessibility of herring food in Quoddy waters and elsewhere in the region would appear dependent upon a determination of the depth at which the fish can and do feed. Precise data concerning the depth at which herring swim are lacking (Battle, Huntsman, et al. 1936, p. 421), but it is reasonable to assume that to feed they will seek the level of most abundant accessible food—and accessibility is dependent upon illumination sufficient to render the food visible enough for capture. Most fishes appear to depend largely on sight in locating and capturing food (Bigelow and Welsh 1924, pp. 416 and 451; Clarke 1936, p. 454).

In regard to depth of visibility in fishes, Grundfest (1932) determined the photosensitivity of the sunfish (*Lepomis*), and Clarke (1936) on this basis has calculated the maximum depths at which this species or others of similar vision could see in various types of water in the western Atlantic. Exact figures are not available for *Clupea,* but in view of its activity and method of feeding, it seems justifiable to assume that its vision is as keen if not keener than that of the relatively slow moving and bottom feeding freshwater sunfish (*Lepomis*). In the following table, prepared by Clarke, data are presented in support of his conclusion that throughout the gulf of Maine and elsewhere in coastal waters vision is possible for such fish from the surface to the bottom.

TABLE XXIX. Maximum depth for vision of fish (similar to Lepomis) in various types of water in the western Atlantic

Types of water	Depth of minimum illumination for vision of fish similar to Lepomis	Depth of water to the bottom
	metres	metres
Deep basin of gulf of Maine	230	165
Georges bank	180	60
Head harbour, bay of Fundy (sta. 5)	190	92
St. Croix river off Robbinston, Me., Passamaquoddy bay	26	26-29 approx.

Records for station 5 and St. Croix river based on observations of Reginald Sawyer.

In relatively shallow areas like the gulf of Maine and bay of Fundy where the depth of the water is considerably less than the depth of minimum illumination for vision of fish (similar to *Lepomis*), the duration of the period of visibility sufficiently clear for the capture of small prey must be proportionately increased (Clarke 1936, p. 454). Thus in the Outer Quoddy region at station 5, where the calculated depth of vision is more than twice the actual depth, feeding even to the bottom would be expected over a reasonably long period during the daylight hours.

If one assumes that Quoddy herring have vision as keen as that of sunfish,

the significance of vertical distribution of zooplankton in the present problem would appear questionable, as the entire water mass would in this case be within the range of visibility. Since this has not been established, however, it is of importance to note that following the onset of vernal augmentation and continuing through the summer of 1932, the maximum volume of zooplankton was at all times found above the 50 metre level (p. 231 and fig. 21), both in the bay of Fundy and gulf of Maine (table III). These records are for the most part based on hauls taken after sunrise and before sunset, in metre nets which allowed all but the more advanced developmental stages of Entomostraca to escape. Considering Clarke's calculations (table XXIX), zooplankton in the upper 50 metres would, during the daylight hours, almost certainly be expected to prove accessible to any fish dependent on keen vision for the capture of food. If this proves to be true, then with the much greater food resources of the offshore areas accessible, added importance is given to the suggestion (p. 318) that the Quoddy herring may not represent a concentration but merely more favourable conditions for fishing.

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The Oxygen-Poor Layer in the Western North Atlantic.

By

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Introduction.

RECENT physical oceanographical investigations have made considerable use of the distribution of oxygen in the sea and have attached particular significance to the minimum oxygen concentration and the oxygen-poor layer (both of which occur at mid-depths).

Since the minimum oxygen concentration and the oxygen-poor layer are quantitatively different, it appears pertinent to define them (this paper deals only with the latter) in order that the adoption of a rigid terminology will avoid confusion. The minimum oxygen concentration occurs at mid-depths and is represented graphically by the principal point of inflexion of the curve characterizing the vertical distribution of oxygen. Theoretically, it is confined to a layer of infinitesimal thickness, but practically, observations from "Atlantis" station 2639 (66°23′W., 35°07′N.) have shown that within a distance of approximately 17 metres both above and below the minimum concentration the existing methods in use by oceanographers are not sufficient to detect any change in oxygen concentration. In general, this minimum concentration has been observed to occur between depths of 200 and 900 metres in the Atlantic and has been traced between latitudes 45°S. to 50°N. Its characteristics in the western North Atlantic and the physical significance of its origin have recently been discussed[1]). On the other hand, the oxygen-poor layer is arbitrarily defined as the layer of water which, containing within its borders the minimum oxygen concentration, embraces that part of the water column where oxygen concentrations are lowest.

*) Contribution No. 139 from the Woods Hole Oceanographic Institution.

[1]) Seiwell, 1937.

Description of Oxygen-Poor Layer.

Over a large part of the western North Atlantic the oxygen-poor layer may be conveniently marked out as that part of the water column within which the oxygen content is 60 per cent. or less of the amount required for saturation at the temperature and salinity of the water if it were at the surface. Thus, in vertical section, the oxygen-poor layer divides the vertical water column into three divisions, or oxygen layers; an upper layer containing the zone of photosynthesis which together with the aid of relatively strong vertical circulation maintains a high oxygen concentration, and the lower oxygen-rich layer where, possibly because of lesser organic oxidation per unit time, the oxygen content is again high.

The range in thickness of the oxygen-poor layer (determined by the position of the isolines of 60 per cent. relative saturation) showed a definite regional variation within the western North Atlantic[2]). In a north-south direction along the 40th meridian ("Atlantis" section B) the thickness of the oxygen-poor layer more or less continuously increased from 0 near latitude 35°N.[3]) to 1100—1200 metres between latitudes 16° and 2°N. Further west, near the longitude of Bermuda, in the north-south direction, the thickness of the oxygen-poor stratum in the convergences off Nova Scotia ranged from 100 to 300 metres, and southward to the latitude of Bermuda it was, in general, 200 to 300 metres thick, while still further south it increased continuously in thickness to more than 500 metres at about latitude 20°N. Still further west, in the American coastwise convergences, the thickness of the oxygen-poor layer decreased rapidly, and, at the latitude of Chesapeake Bay, the layer (so defined) appeared to actually disappear in the convergence, but further westward again expanded to approximately 300 metres thickness.

In mid-Atlantic, north of 40°N., the oxygen-poor layer, as defined by the isolines of 60 per cent., rapidly came to an end (at about 42°—43°N.) due to the presence of oxygen-richer water at mid-depths, and the layer is redefined on the basis of the positions of the 70 per cent. isolines. This oxygen-poor layer was about 500 metres thick at latitude 40°N. and slowly diminished in thickness to about 250 metres at latitude 45°N. and then gave out just north of latitude 49°.

Within the western North Atlantic the regional variation in thickness of the oxygen-poor layer bears certain definite relationships to

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[2]) Seiwell, 1934.

[3]) In mid-Atlantic, along the 40th meridian, "Atlantis" stations 2485 to 2488 have shown the existence of a thin layer of water, about 100 metres thick, whose centre rises from about 900 metres to 600 metres between latitudes 39°30′N. and 42°30′N., and whose oxygen content is less than 60 per cent. saturated. A recent study of the minimum oxygen concentration in the western North Atlantic has suggested that the absence of water less than 60 per cent. saturated in the vicinity of latitude 35° ("Atlantis" stations 1157, 1158) is due to the presence of Mediterranean water which has a relatively high oxygen content for the depths in question (Seiwell, 1937).

the regional variation of depth of its upper boundary. In the north-south direction along the 40th meridian with increasing thickness of the layer the depth of the upper boundary decreased from 600 to 800 metres between 35°N. and 25°N. to less than 200 metres between latitudes 16° and 2°N.; a minimum depth of 75 metres characterized the situation of the upper boundary of the oxygen-poor layer at 8°N. From east to west across the central part of the western Atlantic basin (about latitude 35°N.) as far as the American coastwise convergence, the depth of the upper boundary lay generally between 600 and 800 metres, corresponding to a fairly constant thickness (100 — 300 metres) of the oxygen-poor layer, but, within the convergence, as the oxygen-poor layer thinned, the upper boundary rose rapidly surfaceward from depths of 600—700 metres to less than 200 metres; west of the convergence the upper boundary persisted at about 200 metres as the thickness of the oxygen-poor layer increased.

Consumption of Oxygen in the Oxygen-Poor Layer.

A method for calculating oxygen consumption in the oxygen-poor layer of mid-North Atlantic was based on the results of "Atlantis" observations between the equator and 32°N. along the 40th meridian

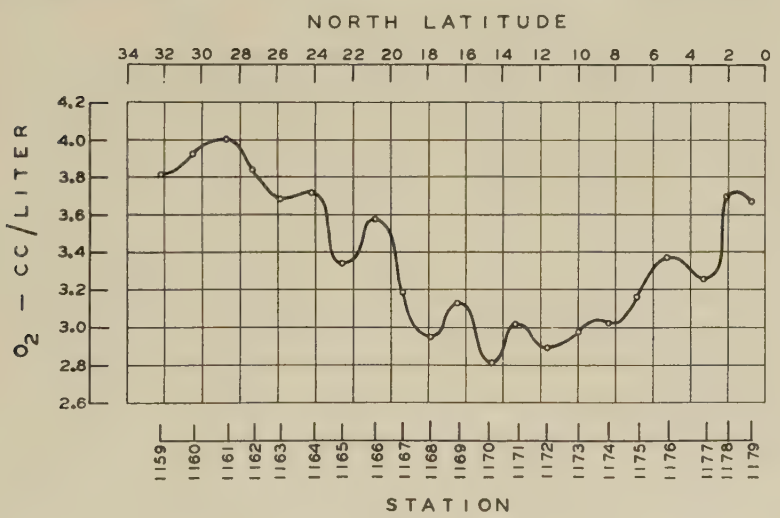

Fig. 1.
Average oxygen content (c.c./litre) of the oxygen-poor layer in mid-Atlantic between 34°N. and equator as determined for "Atlantis" observations. (See text.)

[4]) This periodicity has been assumed to arise as a result of seasonal variation of phytoplankton growth (in regions where the water masses originate) causing variations in oxygen content of the surface water which continue to persist (under certain conditions) in the water mass after it has been shut off from contact with the surface layer and been removed great distances from the origin regions.

(stations 1159—1179) where its average oxygen content (both absolute and relative values) showed a series of undulating values (maxima and minima) suggesting a periodic variation in the oxygen supply[4]) to this layer (Fig. 1). The trend of the average oxygen content declined both from the north and the south, reaching the lowest average value at about latitude 15°N., suggesting that the water masses making up the oxygen-poor layer in this region were mainly of two origins. And support for this possibility was found in determination of the mean salinity anomaly[5]), which showed that one type of water having an anomaly range of 0·05‰ to —0·08‰ characterized the minimum oxygen layer between latitudes 34°N. and 18°N., while a second type with anomaly ranging from —0·31‰ to —0·39‰ characterized the layer between latitudes 12° and 1°N. Hence it appeared that the principal water mass making up the minimum oxygen layer to the north of 18°N. originated in northern latitudes and was spreading southward, and that south of 12°N. it originated in high southern latitudes and was spreading northward; between 12°N. and 18°N. there was a mixing and counteraction of these two water types.

The final assumptions made in the consumption calculation are: (a) that the distance between successive maxima or successive minima of the mean oxygen content represents the mean annual distance the water of the oxygen-poor layer had moved in a north-south direction[6]), and (b) that the decline in amplitude from one maxima or minima to the next succeeding maxima or minima is due to oxygen consumption as the water was displaced an equal horizontal distance (the effect of lateral and vertical mixing may be disregarded for purposes of calculation). Use of the former assumption gave the mean, approximately north-south, component of this layer to be 1·4 centimetres per second; and use of the latter gave the average annual oxygen consumption between latitudes 32°N. and 15°N. to be 0·34 to 0·63c.c. per litre, and between 11° and 0° to be 0·31 to 0·42c.c. per litre. The mean of all values was 0·42c.c. per litre per year, representing a mean annual reduction of about 13 per cent. of the amount of oxygen present in the oxygen-poor layer.

Because of the assumptions involved these results do not have a high degree of accuracy and may deviate significantly from the true values, but since they are the only ones available on oxygen consumption in the deep ocean basins, they may, within reasonable limits, be accepted until further investigation reveals more satisfactory methods. The validity of the results primarily depends on the ability of the water masses to retain seasonal oxygen changes for great distances from their origin regions, but this question must remain

[4]) See p. 279.

[5]) This calculation of salinity anomaly was made according to the average relation between temperature and salinity of the North Atlantic as found by Helland-Hansen (Helland-Hansen, 1930).

[6]) Each oscillation of the mean oxygen curve for the minimum oxygen layer is fixed by three to five points (representing three to five stations) which are sufficient to determine the form of the curve within reasonable limits.

unanswered at present. Other questions which have arisen concerning the validity of the observed oxygen maxima and minima are based on possibilities of error of the oxygen determination and on the effects of short-period vertical oscillations. However, with regard to the former the reality of the maxima and minima (plotted in Fig. 1) is shown because the average difference of 0·25c.c. per litre between an oxygen maximum and its succeeding minimum is more than eight times the probable error of the oxygen titration (±0·03c.c. per litre).

Since the oxygen-poor layer is not referred to any fixed level (being bounded by isolines of 60 per cent. saturation) the effect of vertical oscillations of the water column on its average oxygen content can enter only in so far as such oscillations produce convergences and divergences of the layer itself (due to vertical variations of amplitude and phase of the oscillations; S e i w e l l, 1937). It is conceivable that a convergence of the minimum oxygen layer might squeeze out the oxygen-poorest water, thus raising the average oxygen content of the entire minimum layer, or a divergence might admit oxygen-poor water, thus lowering the average oxygen content of the entire layer. However, it is highly improbable that a situation due to vertical oscillation of the water mass could occur in such a way as to correspond with the time of sampling and produce the observed regular occurrence of the

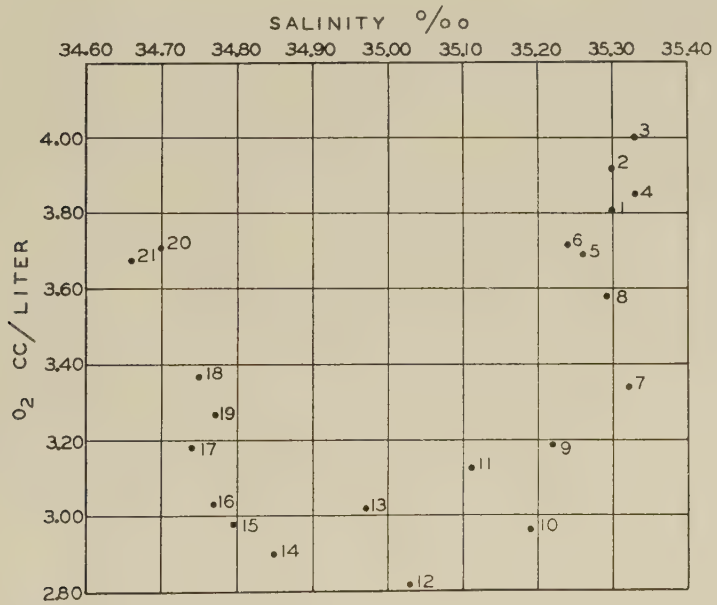

Fig. 2.
Average oxygen (c.c./litre)-salinity (°/oo) correlation in oxygen-poor layer in mid-Atlantic between latitude 34°N. and equator based on "Atlantis" observations. Figures 1 to 21 refer respectively to stations 1159 to 1179.

undulations along the 40th meridian over a distance approximately 2,000 miles northward from the equator (Fig. 1). The agreement of the trend of the average oxygen values with the observed hydrographic conditions is too significant to be disregarded, and, furthermore, no evidence for short period oscillations is shown by the average oxygen-salinity correlation for the minimum oxygen layer (Fig. 2).

The question of seasonally conditioned variations of oxygen and other oceanographic characteristics in subsurface water masses has been recently discussed by Wüst (1935) and he concluded that it is questionable if variations of oceanographic factors in the "Kernschichten" (nuclei) of the subantarctic intermediate water and the upper and middle North Atlantic deep water are conditioned by seasonal variations at their origin regions. In support of this, Wüst uses various examples of what appear to be aperiodic variations of oceanographic characteristics which may be caused by changes in the circulation, by pulsations of the water masses, and also by deviations of stations from the principal axes of outspreading water masses (the latter refers to his conception of the Atlantic circulation). However, for the case under consideration, it appears extremely unlikely that the regular series of oscillations within the minimum oxygen layer could be entirely aperiodically conditioned over a distance of approximately 2,000 miles, and it must be admitted that the evidence is just as deficient to support an aperiodic contention as it is to support the idea of seasonally conditioned oscillations.

Evidence that the southern half of the oxygen-poor layer in mid-North Atlantic (between 35°N. latitude and the equator) occurred chiefly within the remnants of subantarctic water, which penetrated into the southern part of this ocean, and also that the northern half of this layer was influenced by Mediterranean water having a south component is obtained by comparing Iselin's chart of salinity anomalies, for "Atlantis" mid-North Atlantic section of 1932 (stations 1157—1179)[7]), with the chart of the minimum oxygen layer in this same oceanographic section[8]). It is seen that south of 20°N. large negative salinity anomalies characterize the vertical position occupied by the oxygen-poor layer, whereas north of 25° there are high positive salinity anomalies, and between 20°N. and 25°N. the two influences appear to counteract each other. Also, in the southern half of this section the minimum oxygen concentration lay close to the depths of the maximum salinity anomaly and the intermediate salinity minimum, the latter characteristic (which between 0° and 22°N. in this section generally occurs between depths of 700 to 800 metres) marks, according to Wüst's (1935) conception, the nucleus of the subantarctic water entering the North Atlantic[9]).

[7]) Iselin, 1936, page 89, Fig. 55.
[8]) Seiwell, 1934, page 13, Fig. 6.
[9]) Wüst (1935) places the principal axis of outspreading of subantarctic water to the west of the "Atlantis" mid-Atlantic oceanographic section.

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A CONTRIBUTION TO THE CHEMISTRY OF THE CARIBBEAN AND CAYMAN SEAS[1]

NORRIS W. RAKESTRAW AND HOMER P. SMITH

Metcalf Chemical Laboratory of Brown University and the Woods Hole Oceanographic Institution.

INTRODUCTION

During the 1933 Caribbean cruise of the "Atlantis," jointly sponsored by the Woods Hole Oceanographic Institution and the Bingham

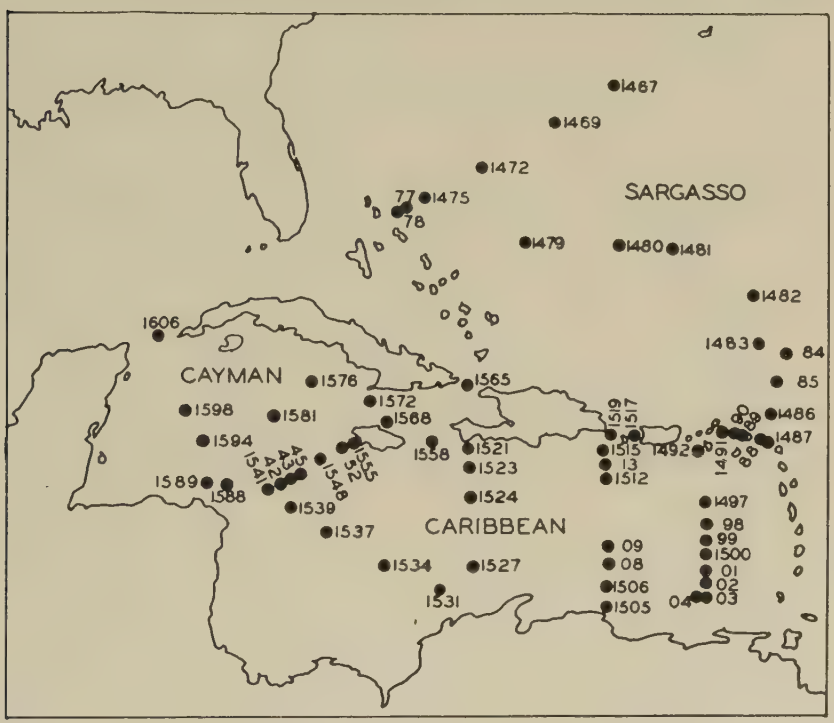

Figure 1. Location of Stations.

Oceanographic Laboratory of Yale University, a number of chemical analyses were made on board in addition to those used for the purely

[1] Joint contribution from the Woods Hole Oceanographic Institution (No. 140), Metcalf Chemical Laboratory of Brown University, and Bingham Oceanographic Foundation of Yale University.

TABLE 1.

CALCULATED VALUES FOR CARBON DIOXIDE FUNCTIONS: FREE CARBON DIOXIDE (C_{CO_2}), TOTAL CARBON DIOXIDE ($C_{\Sigma CO_2}$), CARBONATE ($C_{CO_3^=}$), BICARBONATE ($C_{HCO_3^-}$) IN MOLAR UNITS, CARBON DIOXIDE TENSION (P_{CO_2}), IN ATMOSPHERES

Station	D m	Alk.	Alk. cor.	pH	T	Cl	S	P_{CO_2} x 10^{-4}	C_{CO_2} x 10^{-5}	$C_{HCO_3^-}$ x 10^{-3}	$C_{CO_3^=}$ x 10^{-3}	$C_{\Sigma CO_2}$ x 10^{-3}	O_2
1465	0	2.438	2.438	8.27	20.0	20.6	37.1	2.0	0.7	1.42	0.51	1.94	5.58
	88	2.510	2.510	8.18	20.1	20.6	37.1	2.8	0.9	1.59	0.46	2.06	5.20
	2173	2.363	2.394	8.07	3.9	19.6	35.4	3.2	1.8	1.73	0.34	2.09	6.59
1467	0	2.373	2.373	8.27	20.7	20.6	37.2	1.95	0.6	1.38	0.50	1.89	5.22
	100	2.419	2.419	8.25	20.6	20.6	37.2	2.1	0.7	1.43	0.50	1.94	5.27
	4437	2.378	2.422	8.07	2.6	19.5	35.4	3.1	1.9	1.71	0.36	2.09	6.21
1469	0	2.402	2.402	8.11	21.0	20.7	37.3	3.3	1.1	1.60	0.40	2.01	5.17
	100	2.419	2.419	8.28	20.0	20.6	37.2	1.95	0.7	1.41	0.51	1.93	5.14
	578	2.386	2.393	8.22	15.4	19.9	35.8	2.9	1.1	1.53	0.43	1.97	4.12
	768	2.380	2.387	8.08	10.6	19.8	35.7	3.5	2.0	1.73	0.33	2.08	3.52
	1104	2.347	2.360	8.11	5.6	19.7	35.6	2.95	1.6	1.73	0.32	2.07	5.15
	1888	2.338	2.358	8.13	3.9	19.7	35.6	2.75	1.5	1.70	0.33	2.05	6.20
	2798	2.346	2.376	8.14	3.3	19.7	35.6	2.6	1.5	1.65	0.38	2.05	6.11
	3806	2.346	2.386	8.14	2.8	20.3	36.6	2.45	1.4	1.59	0.38	1.98	6.20
1482	0	*	2.381	8.30	24.0	20.2	36.5	1.9	0.58	1.33	0.53	1.87	4.85
	100	2.406	2.406	8.30	23.8	20.4	36.8	1.9	0.58	1.32	0.54	1.87	4.84
	500	2.367	2.372	8.12	14.5	19.9	36.0	3.2	1.26	1.65	0.36	2.02	4.06
	994	2.384	2.394	8.00	6.5	19.4	35.0	4.3	2.20	1.90	0.27	2.19	3.65
	1942	2.384	2.405	8.11	3.7	19.4	35.0	2.95	1.64	1.76	0.33	2.11	5.80
	2940	2.335	2.365	8.12	2.8	19.4	35.0	2.8	1.62	1.69	0.35	2.06	5.74

1527	0	2.355	2.355	8.14	25.8	20.2	36.6	3.2	0.92	1.49	0.43	1.93	4.68
	100	2.389	2.389	8.11	21.8	20.3	36.7	3.4	1.09	1.59	0.40	2.00	3.55
	500	2.310	2.315	7.95	8.1	19.4	35.0	4.9	2.37	1.88	0.22	2.12	2 75
	986	2.322	2.332	7.98	4.9	19.4	35.0	4.3	2.31	1.88	0.23	2.13	4.09
	1985	2.335	2.356	8.02	4.1	19.4	35.0	3.8	2.11	1.82	0.27	2.11	4.89
	2985	2.347	2.377	8.02	4.1	19.4	35.0	3.7	2.06	1.78	0.30	2.10	4.78
1548	0	2.319	2.319	8.15	26.7	19.9	36.0	2.95	0.82	1.44	0.44	1.89	
	100	2.355	2.355	8.15	25.8	20.1	36.3	3.0	0.85	1.47	0.45	1.93	
	398	2.310	2.315	7.97	11.1	19.6	35.4	4.7	2.07	1.82	0.25	2.09	
	788	2.298	2.308	7.98	5.0	19.3	34.8	5.4	2.90	1.85	0.23	2.11	
1581	0	2.355	2.355	8.17	28.0	20.0	36.1	2.9	0.80	1.43	0.46	1.90	4.75
	100	2.368	2.368	8.18	25.9	20.0	36.1	2.8	0.81	1.45	0.46	1.92	4.74
	500	2.309	2.314	8.00	11.9	19.7	35.4	4.4	1.87	1.77	0.27	2.06	3.30
	989	2.311	2.325	7.96	5.3	19.3	34.9	4.6	2.46	1.88	0.22	2.12	4.09
	1989	2.298	2.318	8.05	4.1	19.4	35.0	3.5	1.93	1.76	0.28	2.06	5.96
	2989	2.298	2.328	8.05	4.1	19.4	35.0	3.4	1.88	1.68	0.31	2.01	
	3989	2.258	2.297	8.04	4.2	19.4	35.0	3.3	1.82	1.65	0.33	2.00	5.88
	4979	2.258	2.305	8.00	4.3	19.4	35.0	3.5	1.95	1.65	0.33	2.00	6.07
	5966	2.229	2.285	7.99	4.5	19.4	35.0	3.5	1.93	1.59	0.36	1.97	5.93
1598	0	2.391	2.391	8.18	27.4	20.0	36.0	2.8	0.79	1.45	0.47	1.93	4.85
	100	2.381	2.381	8.20	26.2	19.9	36.0	2.6	0.75	1.41	0.48	1.90	4.78
	483	2.346	2.351	8.09	11.1	19.6	35.3	3.4	1.50	1.73	0.31	2.06	2.83
	958	2.323	2.333	7.97	5.3	19.3	34.9	4.6	2.47	1.88	0.23	2.13	4.11
	1986	2.310	2.331	8.07	4.1	19.4	35.0	3.2	1.78	1.75	0.29	2.06	5.78
	2976	2.327	2.357	8.05	4.2	19.4	35.0	3.4	1.89	1.73	0.31	2.06	6.12
1606	0	2.367	2.367	8.14	27.2	19.9	36.0	3.2	0.87	1.48	0.44	1.93	4.86
	100	2.344	2.344	8.16	25.0	19.9	36.0	3.0	0.85	1.46	0.45	1.92	4.47
	474	2.296	2.301	7.99	11.9	19.6	35.4	4.4	1.87	1.78	0.26	2.06	3.01

* Data missing. Estimated from Cl.

hydrographic work in the manner which has now become more or less routine in oceanographic investigations. A general description of the cruise and a discussion of the hydrographic results has already been published by Parr (*1*). In the present report an account will be made of the special chemistry of the Caribbean and Cayman Seas with reference to phosphate, nitrate, nitrite, pH and buffer capacity. Serial samples were taken at various depths, from two to twenty or more at a station. In such samples, phosphate was determined at 59 different stations; nitrate at 29; pH at 28; nitrite at 22; buffer capacity, or "alkalinity," at 12. These data have been drawn on for studies on nitrite and buffer capacity which have already been published (*2*, *3*). All the raw data have been made available in the Bulletin Hydrographique (*4*). It is now proposed to correlate and discuss the phosphate, nitrate and pH figures, as well as those for the factors in the carbon dioxide equilibrium, which may be calculated from the pH and alkalinity.

In adapting the originally published data for use in this paper two minor changes have been made: All values for phosphate and nitrate have been converted into terms of milligram atoms per liter (of P and N, respectively), in accordance with the recommendations of the International Council for the Exploration of the Sea, and all pH values have been corrected for depth (*5*), to represent conditions in situ.

To convert phosphate values into milligrams of P_2O_5 per liter multiply by 71; mg. of PO_4, by 95; mg. of P, by 31. To convert nitrate values into milligrams of nitrate-nitrogen per liter multiply by 14.

The methods of analysis used were those which have become standard, for the most part: Atkins' method for phosphate; the Harvey reduced-strychnine method for nitrate; colorimetric method for pH, using cresol red and the bicolorimeter. More detailed information on this last procedure has recently been given by Mitchell and Taylor (*6*), and by Mitchell, Buch and Rakestraw (*7*). The corrections and methods of calculation used are explained in the source of the original data (*4*).

Figure 1 shows the location of stations at which chemical analyses were made. Although it contains fewer stations than Parr's complete list for the Caribbean, it includes a number of additional stations in the western Sargasso Sea, during the earlier part of the cruise.

Table 1 gives the calculated results for the tension and concentration of carbon dioxide, and the concentrations of carbonate, bicarbonate and total carbon dioxide. These have been calculated from the equations and tables of Buch and others (*5*, *8*, *9*).

VERTICAL DISTRIBUTION

Figures 2 to 9 present vertical station curves for the chemical data at a few selected stations. These are not only chosen to be representative of different areas, but also include those at which the most extensive observations of the carbon dioxide equilibrium were made. Oxygen curves are also drawn in some

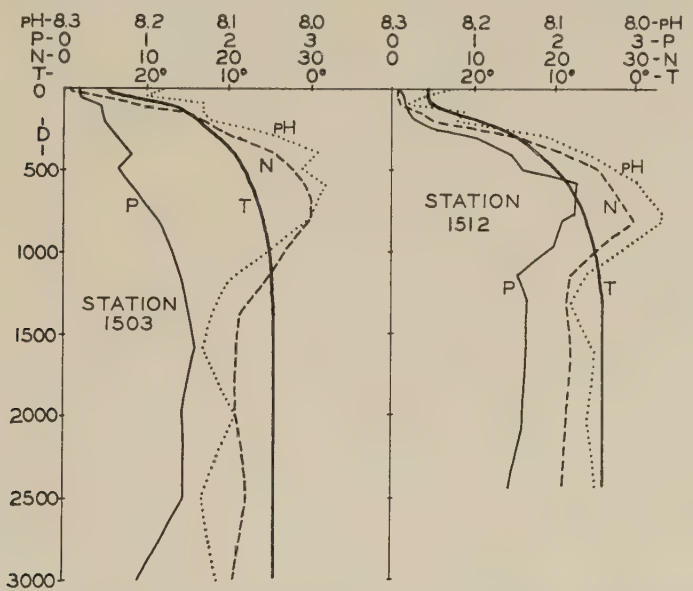

Figure 2. Vertical distribution of temperature (T), phosphate (P), nitrate (N) and pH at Stations 1503 and 1512. Depths vertically in meters. Phosphate and nitrate in milligram atoms per liter.

cases, for comparison. Stations 1469 and 1482 are generally representative of the Sargasso, Nos. 1503, 1512 and 1527 represent the Caribbean proper, and 1581, 1598 and 1606 the western basin which Parr (*1*) has named the Cayman Sea. Nos. 1558 and 1572 are included because of their adjacency to the Windward Passage, at which special conditions sometimes obtain.

The most striking condition at Station 1503 is the unusually low phosphate above 1500 meters, although nitrate is of normal magnitude. This exception is discussed later.

The general character of these curves is the same as found invariably in the deep water of the Atlantic, and elsewhere. The zone of maximum phosphate and nitrate, and of minimum pH, falls between 600 and 1000 meters, usually at about 800. It is clearly associated with the most extreme part of the thermocline. In fact, close inspection shows it to coincide very closely, in the Carib-

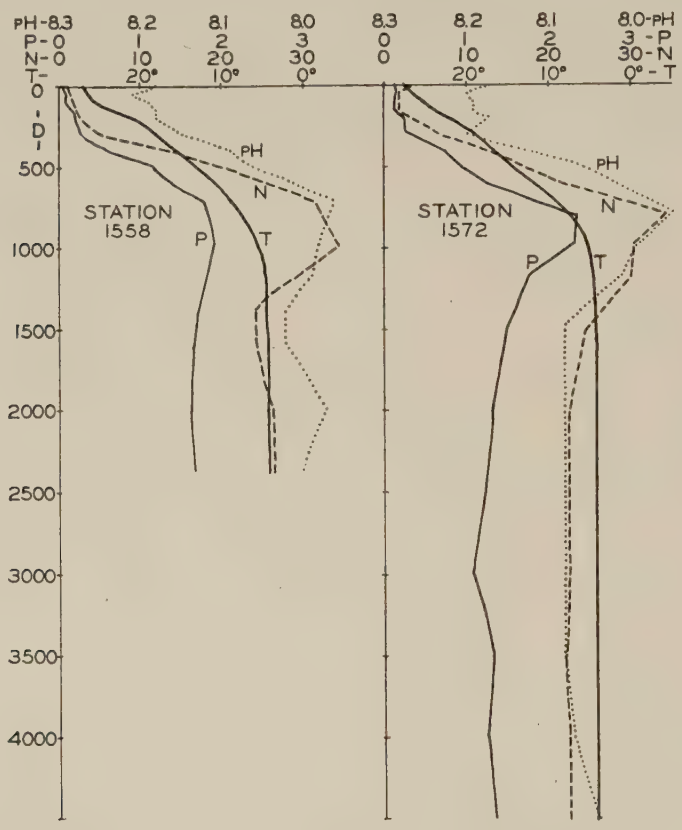

Figure 3. Vertical distribution of temperature (T), phosphate (P), nitrate (N) and pH at Stations 1558 and 1572. Depths vertically in meters. Phosphate and nitrate in milligram atoms per liter.

bean at least, with the 7° isotherm. This, in turn, is also the level of minimum salinity and of maximum vertical stability of the water. Such a relation is of course to be expected. The various carbon dioxide functions also converge at this same point, while the level of minimum oxygen is consistently a little higher.

The less pronounced maximum of nitrate and phosphate in the Sargasso is evidently connected with the gentler slope of the thermocline.

Below the maximum zone, from 800 to 1500 meters, phosphate and nitrate diminish, and pH increases, and below this the water is almost, if not completely, homogeneous.

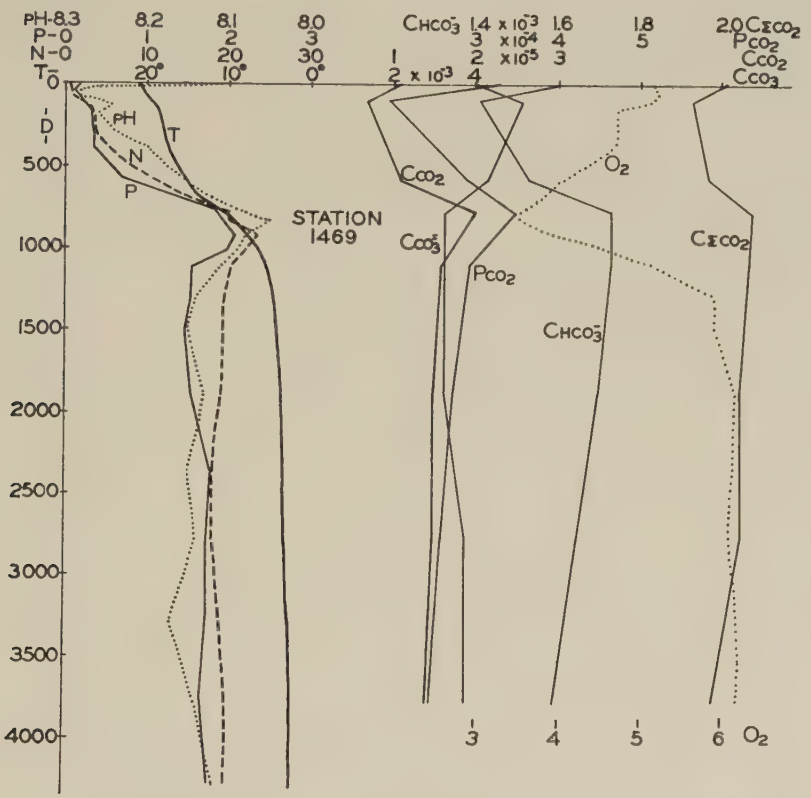

Figure 4. Vertical distribution at Station 1469. Depths vertically in meters. Temperature (T); pH; phosphate (P) and nitrate (N), in milligram atoms per liter; oxygen, in ml. per liter; free carbon dioxide (C_{CO_2}), total carbon dioxide ($C_{\Sigma CO_2}$), carbonate (C_{CO_3}), bicarbonate (C_{HCO_3}), in molar units; carbon dioxide tension (P_{CO_2}), in atmospheres.

Considering only the higher concentrations, between the maximum zone and the bottom, the atomic ratio between nitrogen and phosphorus is about 16 to 1, a little less than that calculated by Redfield (*10*).

The picture of the carbon dioxide functions is practically the same at all stations, with the exception of the northern Sargasso station, No. 1469, at which total CO_2 was somewhat lower than elsewhere. In every case the carbonate ion concentration increased between its minimum (800 meters) and the bottom.

Samples for these analyses were taken at intervals of every 500 meters. As a result of this the maximum-minimum level was missed by 100 meters or more. This is indicated at Stations 1581 and 1598, where it is particularly apparent, by broken lines in the curves.

The changes in the carbon dioxide equilibrium must be closely related to the distribution of nitrate and phosphate, for they all result from different parts of the general cycle of decomposition and oxidation of organic matter. We are

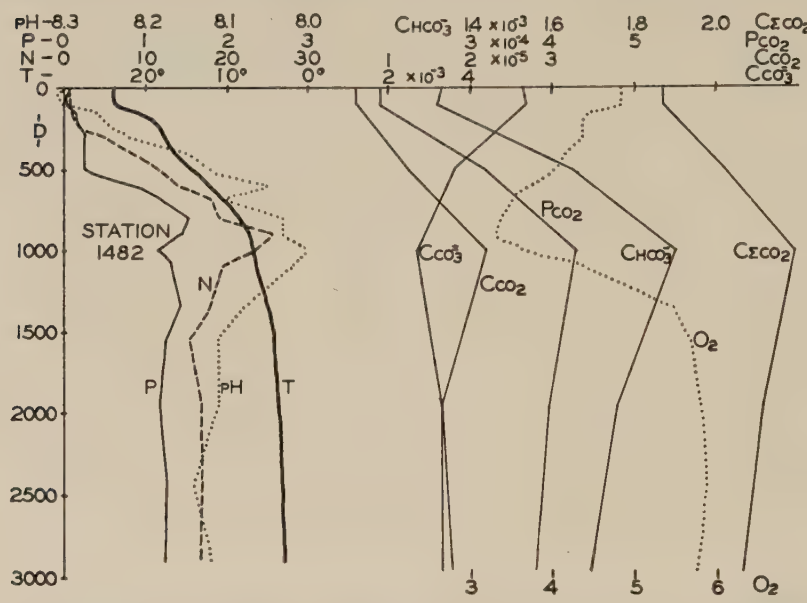

Figure 5. Vertical distribution at Station 1482. Depths vertically in meters. Temperature (T); pH; phosphate (P) and nitrate (N), in milligram atoms per liter; oxygen, in ml. per liter; free carbon dioxide (C_{CO_2}), total carbon dioxide ($C_{\Sigma CO_2}$), carbonate (C_{CO_3}), bicarbonate (C_{HCO_3}), in molar units; carbon dioxide tension (P_{CO_2}), in atmospheres.

not yet in a position to discuss this in detail. It may be pointed out, however, that these values are on the whole consistent with those published by Wattenberg (*11*) for the Atlantic. His data seem to indicate a somewhat lower CO_2 tension (P_{CO_2}) in the western part of the Atlantic then in the eastern, and in this sense the Caribbean is a still further extension, for our values are even somewhat lower, on the average. But since different methods were used in the two studies for the determination of both pH and alkalinity it is hardly safe to compare absolute values. Although we have studied a smaller number of stations the relative picture at each is fully as consistent as those of the "Meteor" stations.

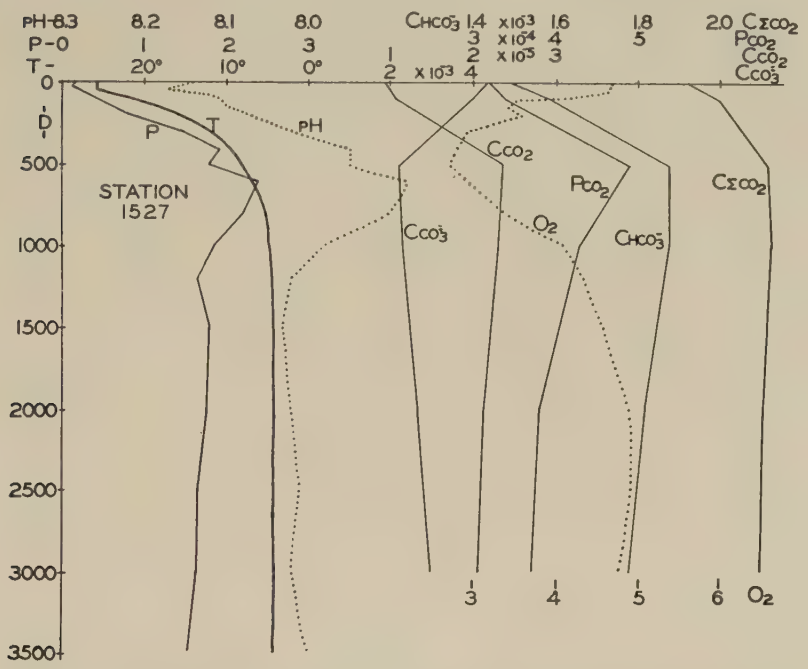

Figure 6. Vertical distribution at Station 1527. Depths vertically in meters. Temperature (T); pH; phosphate (P) and nitrate (N), in milligram atoms per liter; oxygen, in ml. per liter; free carbon dioxide (C_{CO_2}), total carbon dioxide ($C_{\Sigma CO_2}$), carbonate (C_{CO_3}), bicarbonate (C_{HCO_3}), in molar units; carbon dioxide tension (P_{CO_2}), in atmospheres.

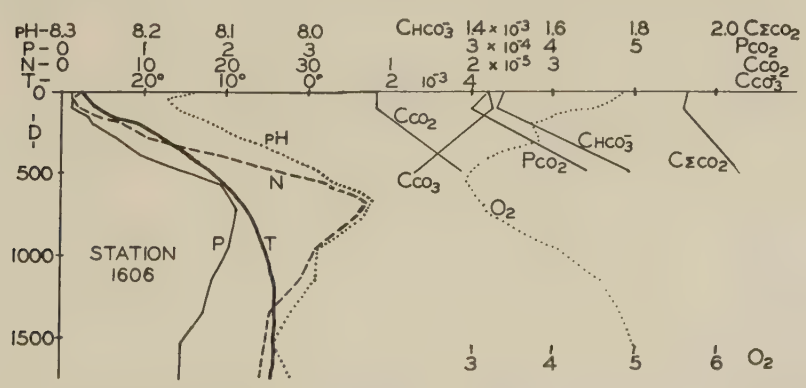

Figure 7. Vertical distribution at Station 1606. Depths vertically in meters. Temperature (T); pH; phosphate (P) and nitrate (N), in milligram atoms per liter; oxygen, in ml. per liter; free carbon dioxide (C_{CO_2}), total carbon dioxide ($C_{\Sigma CO_2}$), carbonate (C_{CO_3}), bicarbonate (C_{HCO_3}), in molar units; carbon dioxide tension (P_{CO_2}), in atmospheres.

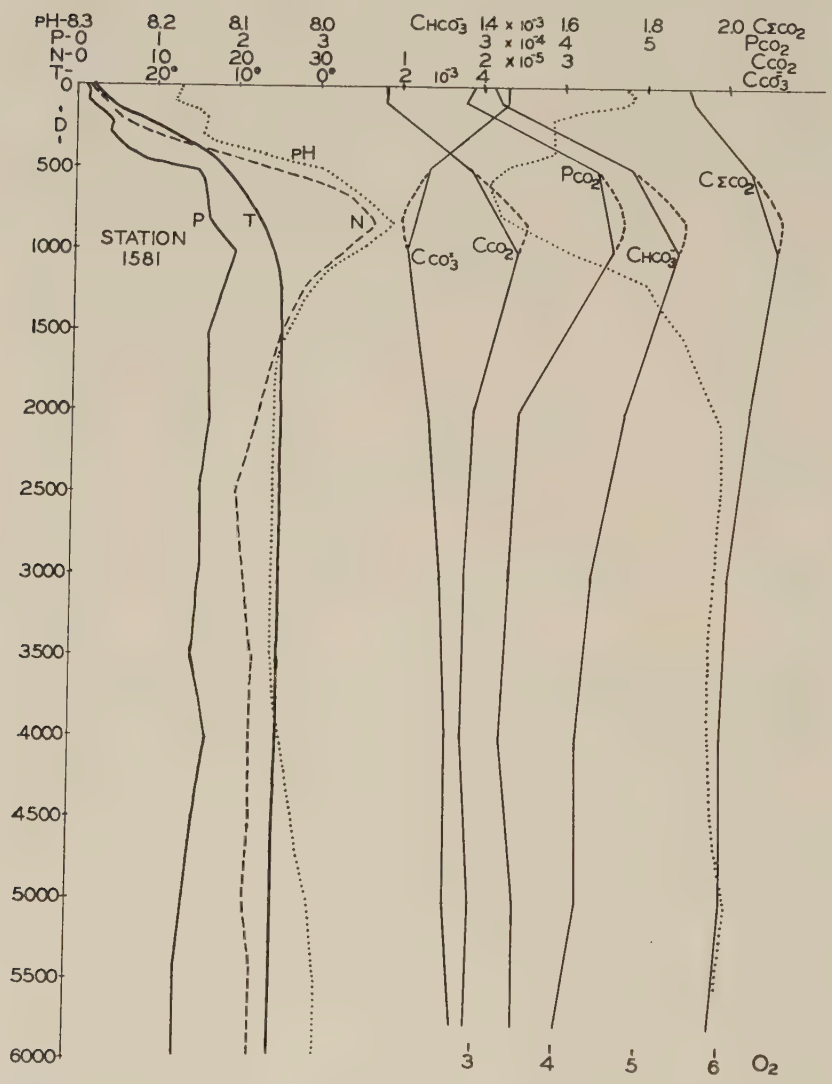

Figure 8. Vertical distribution at Station 1581. Depths vertically in meters. Temperature (T); pH; phosphate (P) and nitrate (N), in milligram atoms per liter; oxygen, in ml. per liter; free carbon dioxide (C_{CO_2}), total carbon dioxide ($C_{\Sigma CO_2}$), carbonate (C_{CO_3}), bicarbonate (C_{HCO_3}), in molar units; carbon dioxide tension (P_{CO_2}), in atmospheres. Broken lines indicate probable maxima and minima of the CO_2 curves.

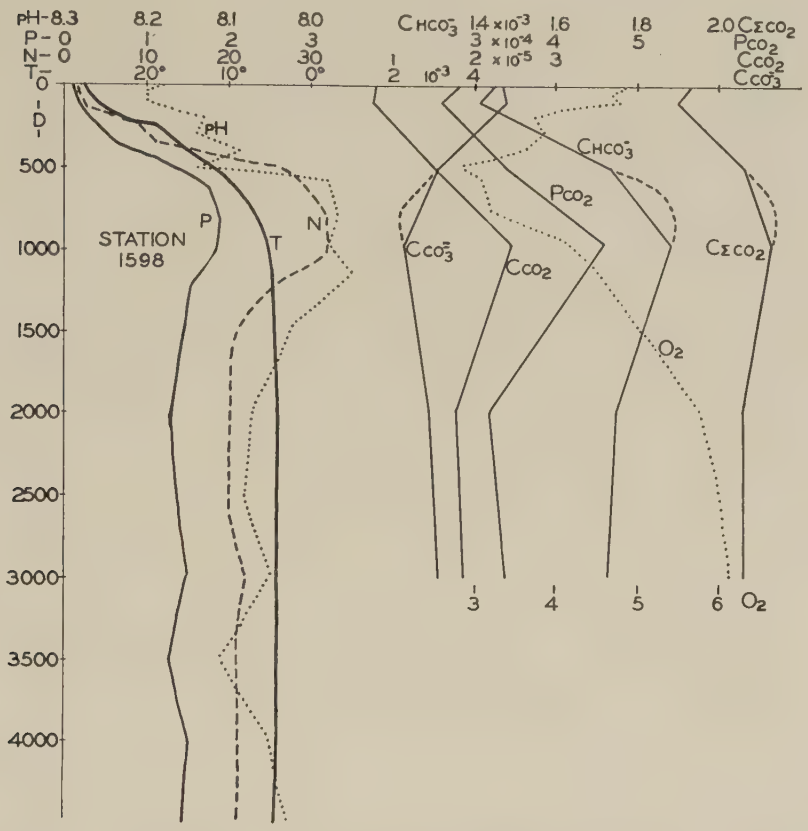

Figure 9. Vertical distribution at Station 1598. Depths vertically in meters. Temperature (T); pH; phosphate (P) and nitrate (N), in milligram atoms per liter; oxygen, in ml, per liter; free carbon dioxide (C_{CO_2}), total carbon dioxide ($C_{\Sigma CO_2}$), carbonate (C_{CO_3}), bicarbonate (C_{HCO_3}), in molar units; carbon dioxide tension (P_{CO_2}), in atmospheres. Broken lines indicate probable maxima and minima of the CO_2 curves.

HORIZONTAL DISTRIBUTION

Figures 10 to 21 show the horizontal distribution of phosphate, nitrate and pH at certain different depths. These depths were chosen to show most clearly the relations through the maximum-minimum layer. Accordingly, it seemed best to plot the data at the surface and at 400, 500, 600, 800, 1000, 2000 and 3000 meters. Since phosphate was determined at about twice as many stations as were nitrate and pH the picture for phosphate distribution is the most comprehensive. Nitrate and pH were generally determined at the same stations. The following general features seem to be apparent in these data:

Phosphate. At the surface, the central area of very low phosphate (less than .10 milligram atoms per liter) suggests an inflow of Sargasso water from the northeast. This is in accordance with Parr's hydrographic findings. Higher surface concentrations are found to the south and west.

At 400 meters the Sargasso water to the north has very little phosphate, but the concentration increases continuously to the South American coast, where the area of highest concentration has no connection with water outside the Caribbean basin.

The intrusion of intermediate water from the north, at 500 meters, which Parr (*1*) found to take place through the Anegada and Windward Passages, seems to be evident here also. High concentrations to the south reach their maximum in the vicinity of the eddy in the Panamanian bight.

At 600 and 800 meters the phosphate concentration throughout the Caribbean area is higher than in the waters to the east and north. The maximum phosphate zone is at about 800 meters, except in the center of the Cayman Sea, where it is somewhat lower. There seems to be some mixing with water from the north through the Windward Passage at this level.

In the Sargasso we find the maximum phosphate at 1000 meters, but in the Caribbean area, except for the center of the Cayman Sea, values are somewhat less than maximal at this depth.

At 2000 meters the Cayman basin is entirely homogeneous, but the Caribbean is not completely so. The higher concentrations are still in the south, for the most part, but reach a maximum in the east. The peculiar conditions in the eastern end of the Caribbean will be discussed later.

At 3000 meters the Caribbean and Cayman basins are practically homogeneous, but somewhat lower concentrations of phosphate occur in parts of the Sargasso.

In general, the Caribbean area is rather richer in phosphate than are the outside waters. This applies to all levels. Unfortunately, the data from this cruise give us no insight into the composition of the north equatorial water, which contributes so largely to the Caribbean, but the figures given by Seiwell (*12*) are regularly lower than those here shown. With due allowance for differences in analytical results by different observers, it seems nevertheless evident that phosphate is actively regenerated by organic decomposition throughout a large part, at least, of the Caribbean, and even more in the Cayman Sea. The effects of circulation and the mixing of water masses are superimposed upon this process.

Nitrate. Values are so low at the surface, throughout, that the only significant feature seems to be the somewhat higher concentration in the Cayman Sea. The slightly lower figures along the coast to the south may indicate a higher rate of biological activity here. This factor is perhaps mainly responsible for the slight differences in concentration, although circulation may also play a part.

At 400 and 500 meters the picture is quite similar to that of phosphate at the same levels. Concentrations are distinctly higher to the south, and there is some indication of the inflow of intermediate water from the northeast and through the Windward Passage.

At 600 meters there is apparently still some inflow from the northeast, and concentrations have considerably increased to the southwest. At 800 meters the maximum zone is reached, which extends over all the southern and western part of the area. Meantime, concentrations in the Sargasso are consistently lower than in the Caribbean, but increase continually down to 1000 meters. At this level in the Caribbean nitrate has diminished considerably, although a zone of high concentration still persists in the northern part of the Cayman Sea.

At 2000 and 3000 meters both basins are quite homogeneous, but nitrate concentration is distinctly higher than in the outside waters. This conclusion is partly presumptive, as there are no data for nitrate in the north equatorial water. But since in the case of the Sargasso the nitrate relation is the same as that for phosphate, it seems safe to assume the same condition for the water to the southeast.

Evidently, therefore, the Caribbean is an area of nitrate regeneration as well as phosphate.

pH. Throughout the Caribbean area pH values at the surface are somewhat lower than in the Sargasso, except for a zone in the northeast, which, again, is probably modified by the inflow of Sargasso water.

At 400 meters distinctly lower values are found to the south. A close relation is of course to be expected between pH and nitrate and phosphate, since the generation of the latter substances results from the oxidation of organic matter. This is accompanied by the formation of carbon dioxide from the simultaneous oxidation of carbon, and increase in acidity (lowering of pH) is the result.

At 500 and 600 meters the minimum zone of pH has moved to the west, where its correspondence with the maximum nitrate is easily seen.

The full extent of the minimum zone occurs at 800 meters except in the Sargasso where it is again somewhat lower. But neither at this level nor at any other are the values in the Sargasso as extreme as those in the Caribbean or Cayman Seas.

At 1000 meters the lowest values are found in the Cayman and western Caribbean, consistent with the behavior of phosphate and nitrate.

At 2000 and 3000 meters both basins are again nearly homogeneous, but the characteristics of the water are distinctly different from that outside.

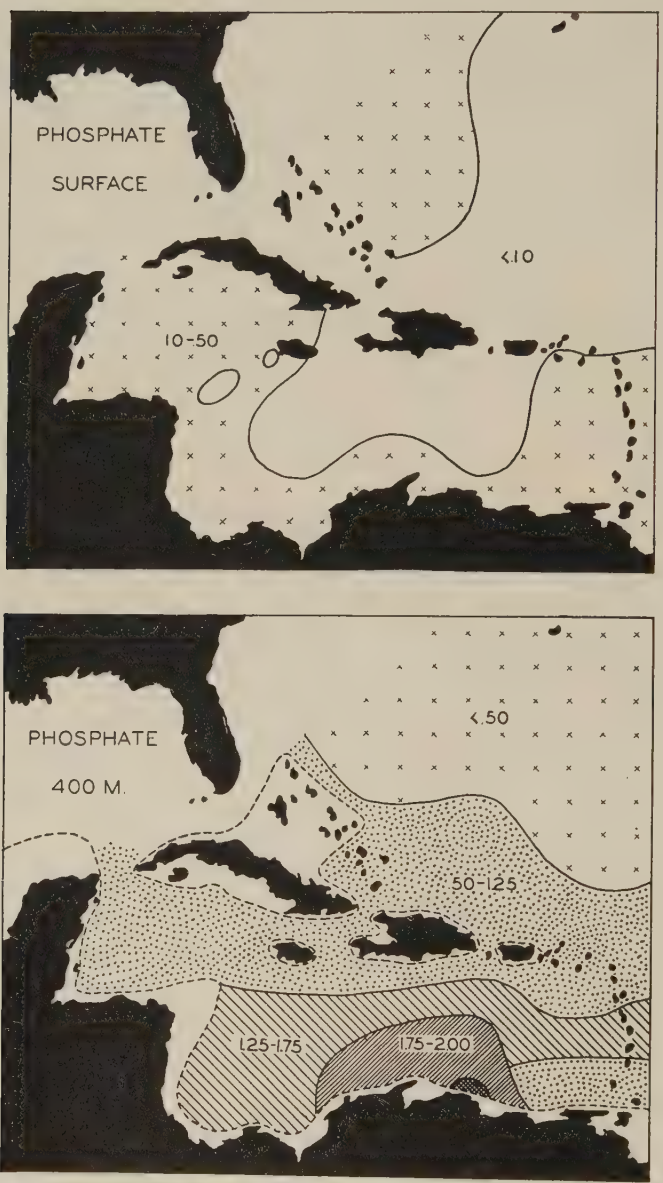

Figure 10. Horizontal distribution of phosphate, at surface and 400 meters. Units, milligram atoms per liter.

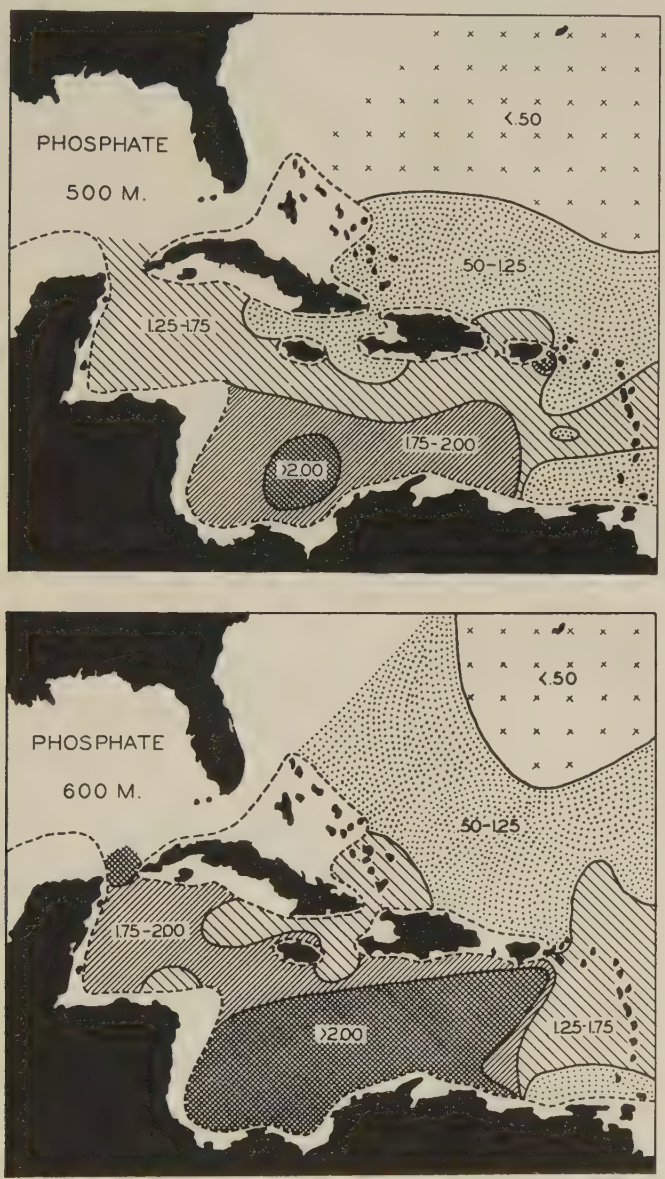

Figure 11. Horizontal distribution of phosphate, at 500 and 600 meters. Units, milligram atoms per liter.

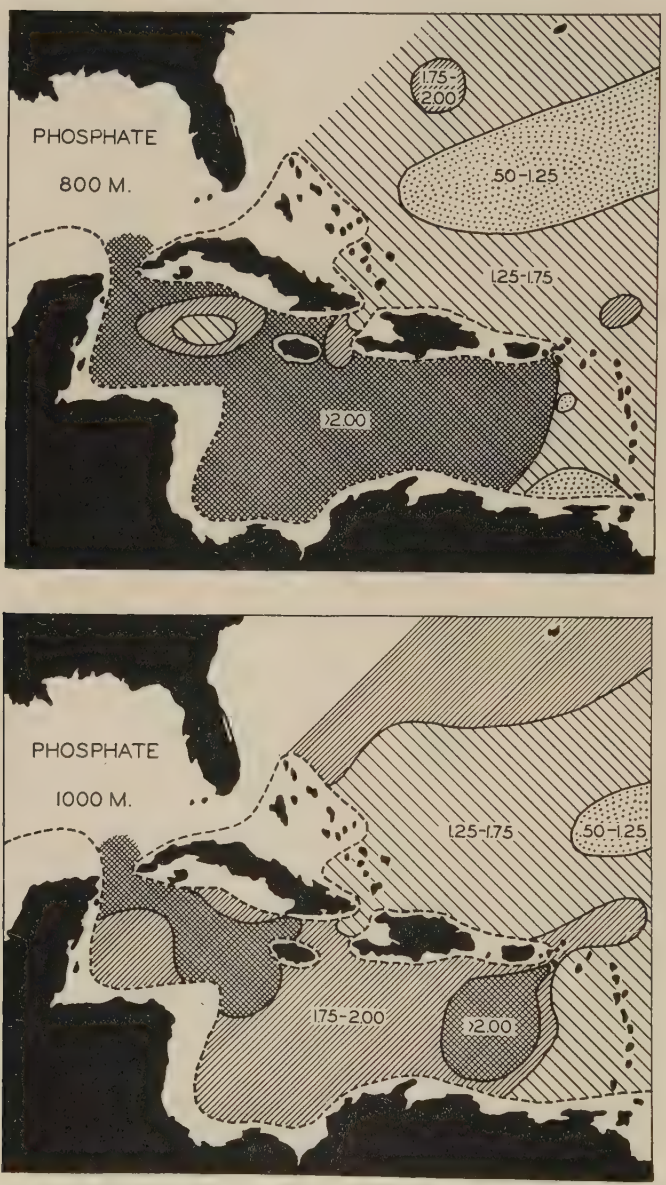

Figure 12. Horizontal distribution of phosphate, at 800 and 1000 meters. Units, milligram atoms per liter.

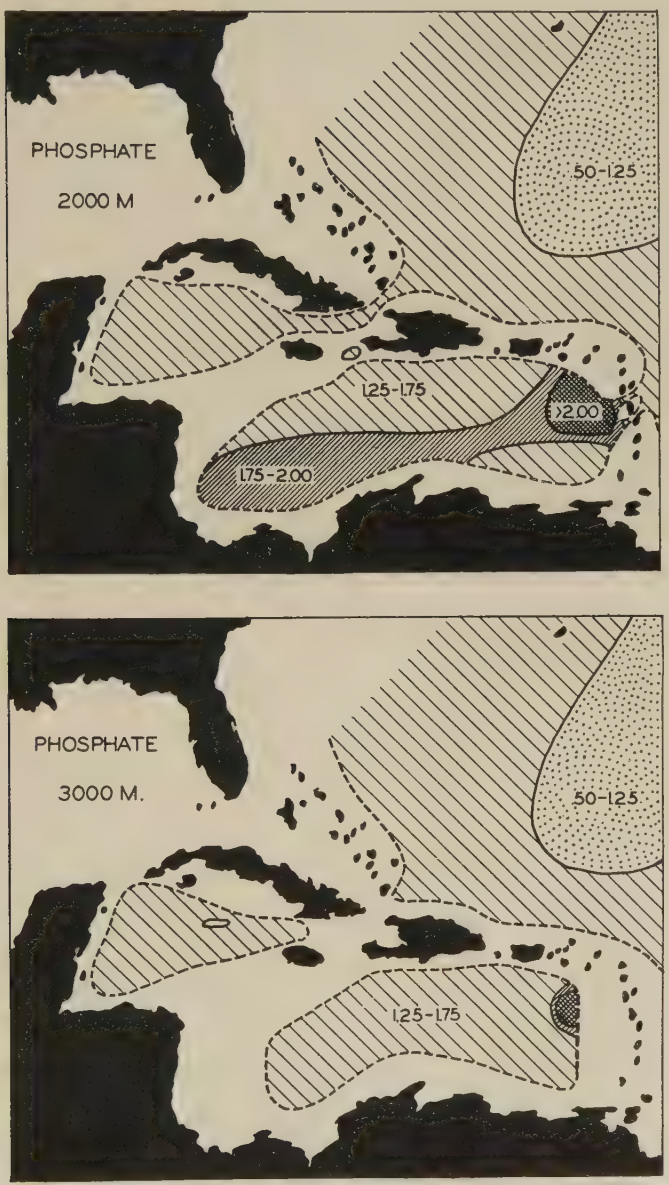

Figure 13. Horizontal distribution of phosphate, at 2000 and 3000 meters. Units, milligram atoms per liter.

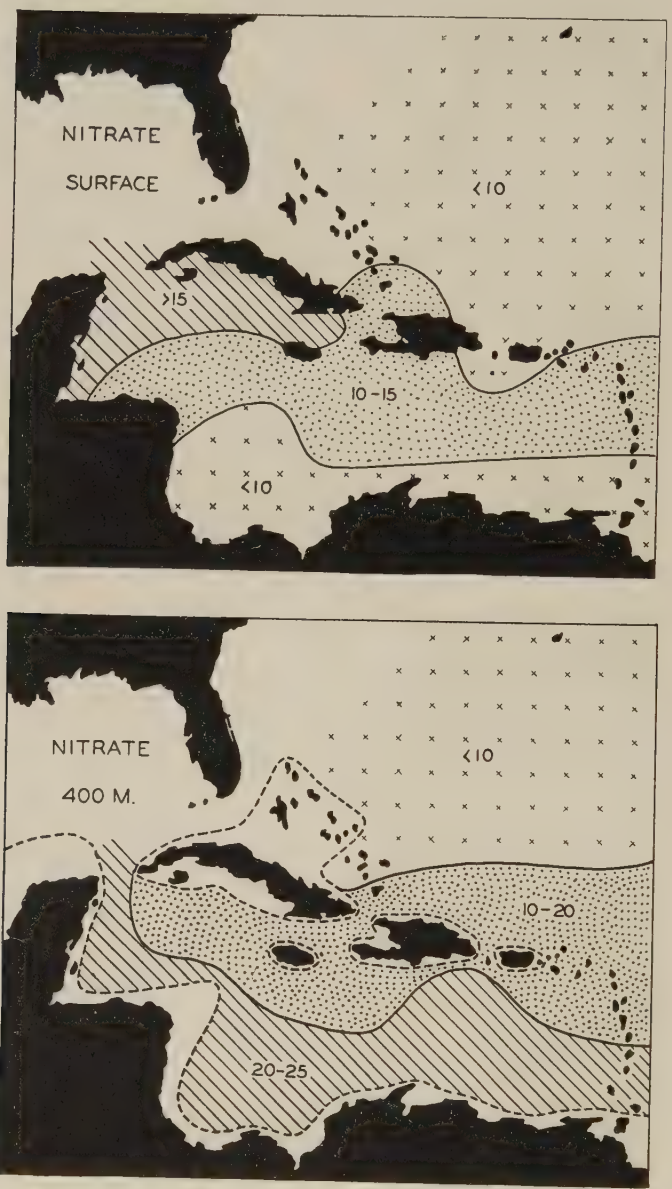

Figure 14. Horizontal distribution of nitrate, at surface and 400 meters. Units, milligram atoms per liter.

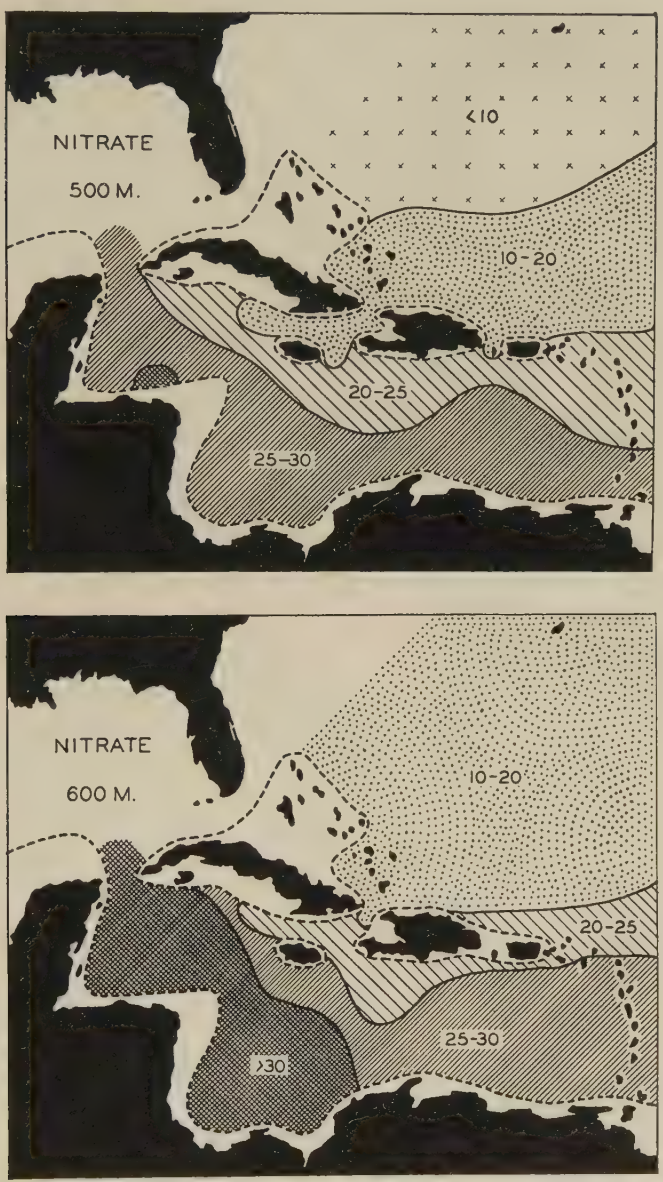

Figure 15. Horizontal distribution of nitrate, at 500 and 600 meters. Units, milligram atoms per liter.

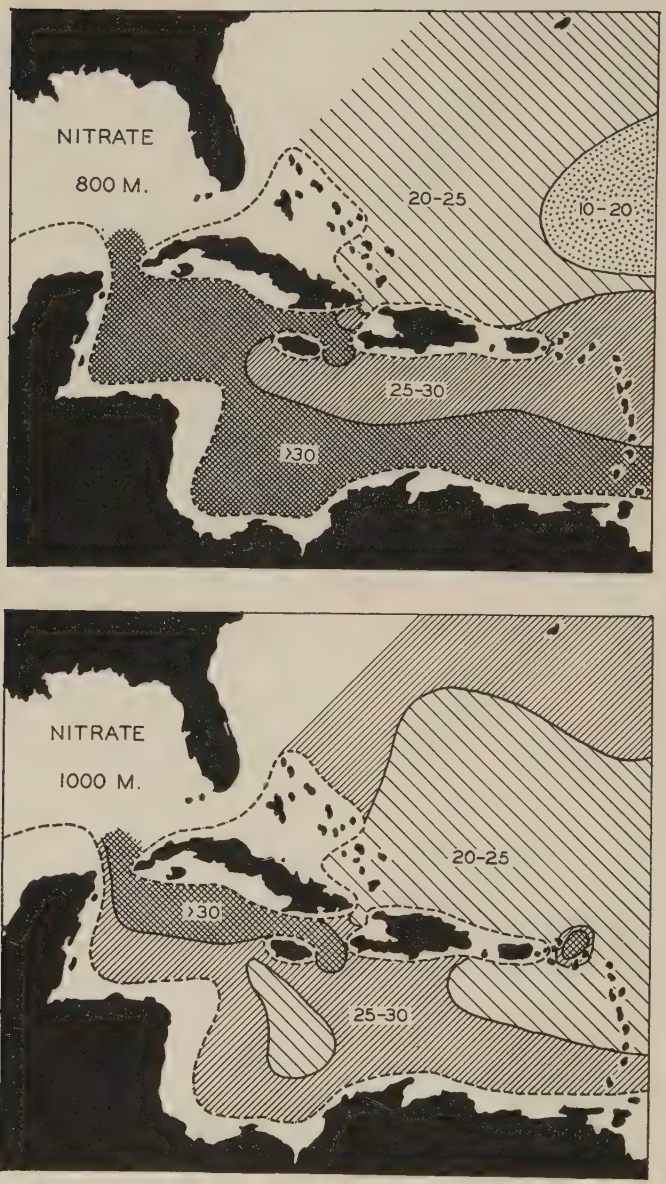

Figure 16. Horizontal distribution of nitrate, at 800 and 1000 meters. Units, milligram atoms per liter.

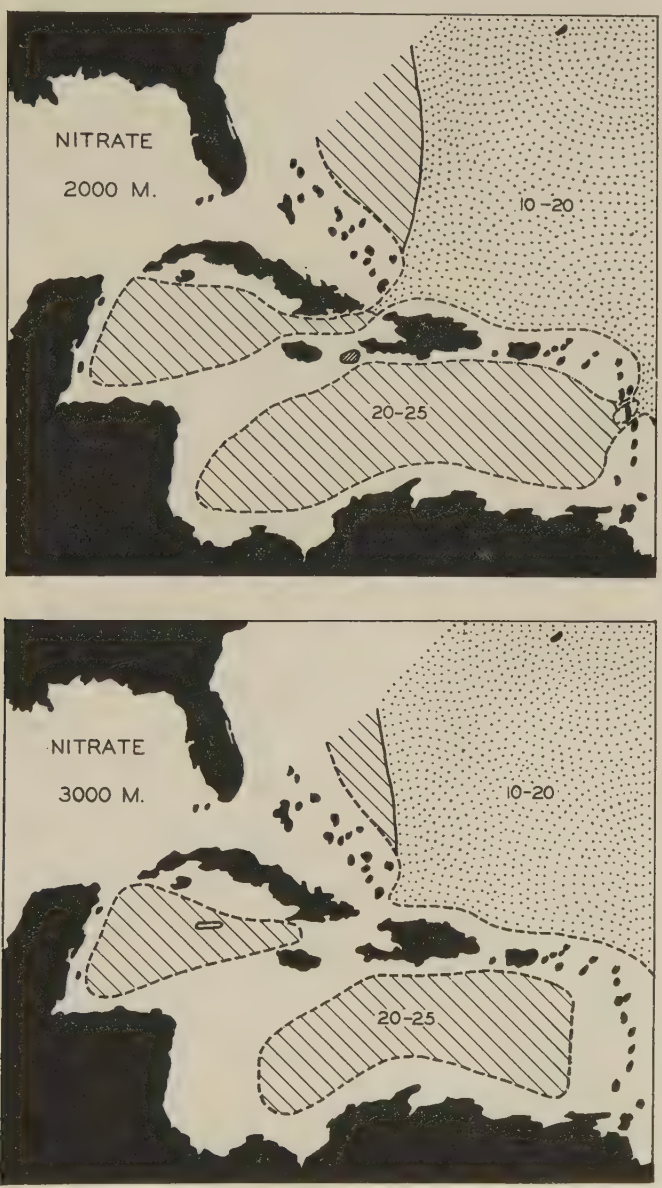

Figure 17. Horizontal distribution of nitrate, at 2000 and 3000 meters. Units, milligram atoms per liter.

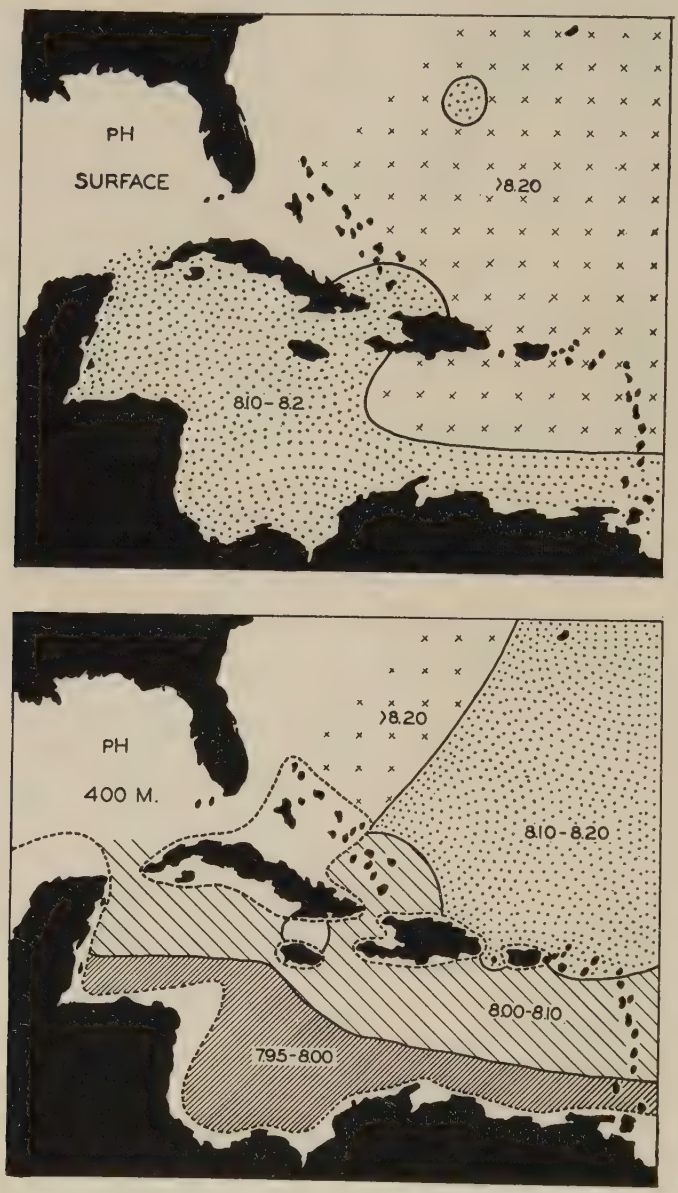

Figure 18. Horizontal distribution of pH, at surface and 400 meters.

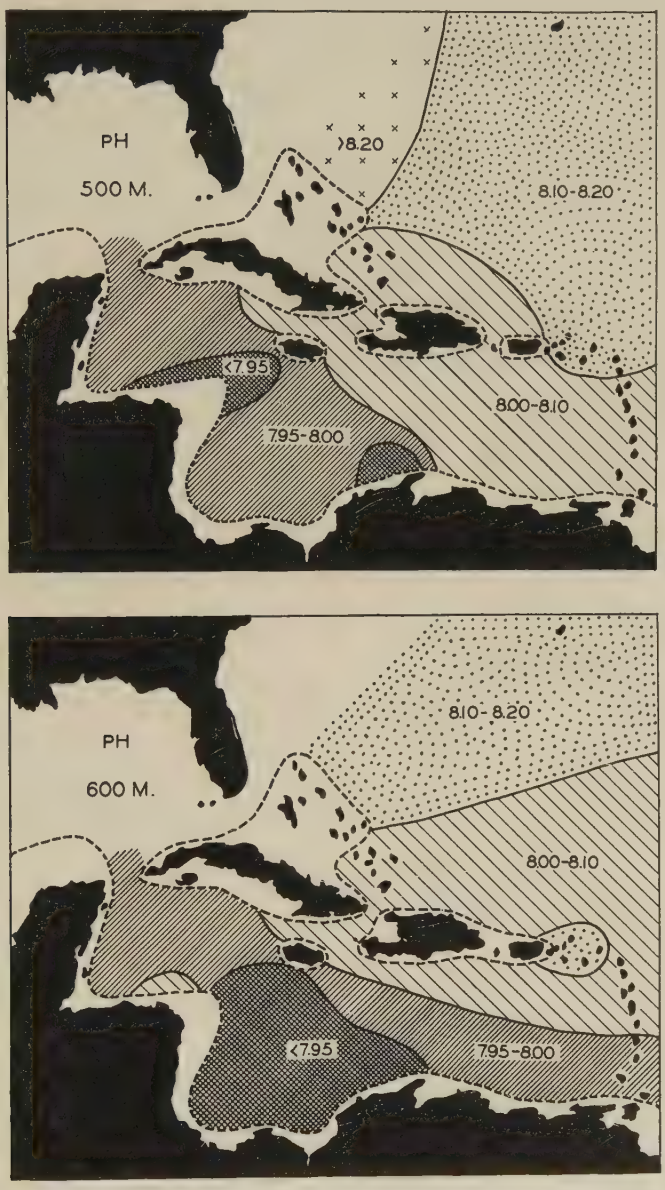

Figure 19. Horizontal distribution of pH, at 500 and 600 meters.

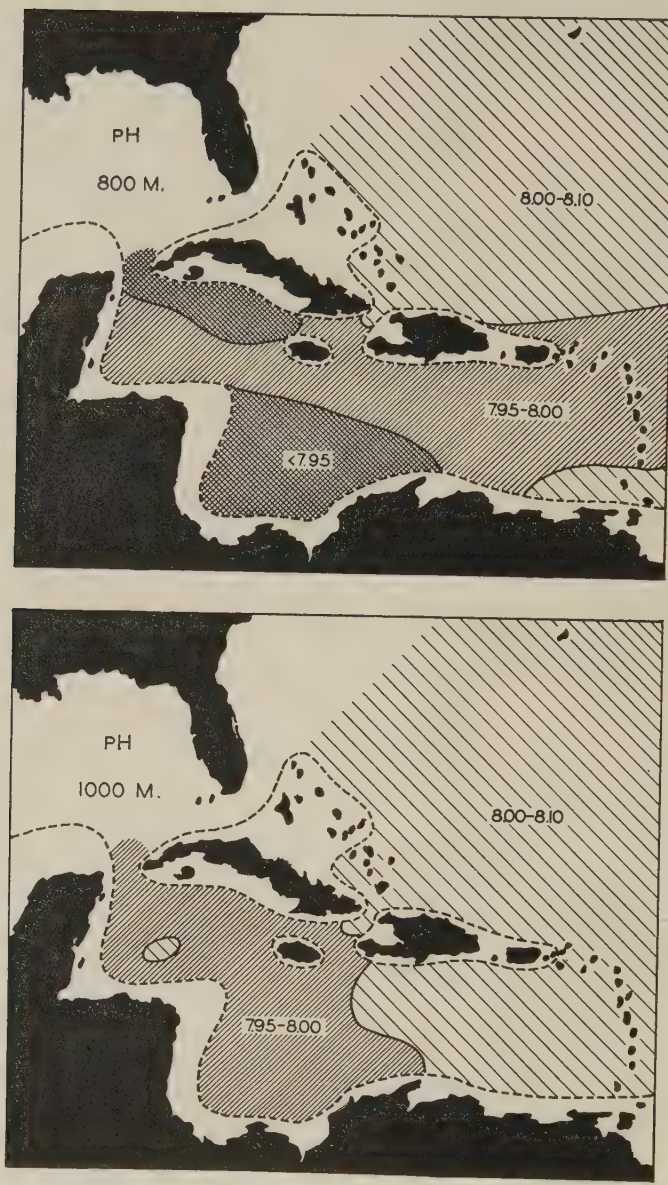

Figure 20. Horizontal distribution of pH, at 800 and 1000 meters.

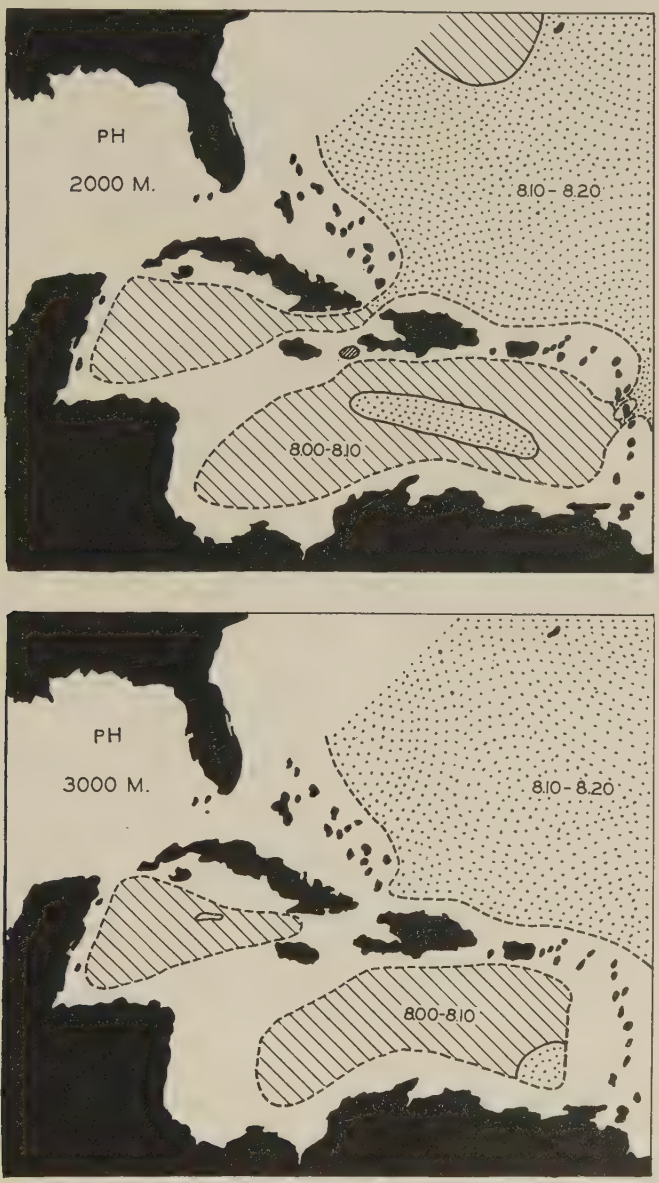

Figure 21. Horizontal distribution of pH, at 2000 and 3000 meters.

RELATION TO TEMPERATURE AND SALINITY

From a consideration of Figures 10 to 21 it is apparent that there is a "sloping" of the whole water mass from north to south. This has been shown by Parr (*1*) to be true also with respect to both temperature and salinity. At any one level consistently lower temperatures are found in the south, with corresponding displacements of salinity. In view of this it seemed advisable to attempt a correlation between the chemical data and either temperature or salinity.

Figure 22 shows nitrate plotted against temperature at a number of stations chosen from the three principal areas, Caribbean, Cayman and Sargasso Seas. In the first two cases all points are included within fairly narrow envelopes, while in the Sargasso there is somewhat more scattering at the lower temperatures. In the upper levels, however, a more consistent relation exists in the Sargasso than in the other areas.

The relation between nitrate and salinity at the same stations is shown in Figure 23. The same sort of qualitative difference is seen between the three areas, but no information is obtained from these curves which was not to be found in the nitrate-temperature relation. Accordingly, since the salinity curve is somewhat more complicated, all subsequent correlations were made to temperature only.

Figure 27 shows the mean curves taken from the envelopes in Figures 22 and 23. Although these relations are obviously not as valuable for diagnostic purposes as are temperature-salinity curves, it is nevertheless evident that a fair characterization of a water mass may often be made in terms of such correlations. Three distinctly different situations can be seen in the three different areas.

An example of the possible use of such relations is to be observed in the case of Station 1565. This station, which lies in the Windward Passage, is on the boundary between the Sargasso area and the Caribbean. An analysis of its nitrate-temperature relation, however, shows that it properly belongs with the Sargasso. The points plotted for this station in Figure 22 would fall far outside the envelope for the Cayman Sea. The situation is reversed, however, at Station 1572, which is somewhat further inside the boundary. This station must obviously be included with the others of the Cayman area.

A similar relation between pH and temperature is shown in Figure 24, and the mean curves from these envelopes, represented in Figure 28, are thoroughly consistent with those for the nitrate-temperature relation.

Since the phosphate figures were more extensive a more detailed analysis of their temperature relation was attempted. The Sargasso stations were divided into two groups: those to the north (Nos. 1467 to 1481) in one group, and those to the east (Nos. 1482 to 1490) in another. The few stations in the Cayman Sea were included in one group as before, but the larger number in the Caribbean were divided into the three N-S profiles (called respectively the East Line, Mid-Line and West Line) and another group of stations constituting a profile roughly E-W across the southern part of the basin. The phosphate-temperature relations for these seven groups are shown in Figures 25 and 26.

The points for the stations in the Cayman Sea, and those in the middle and western N-S profiles in the Caribbean, fall quite satisfactorily within narrow envelopes; those for the stations on the E-W profile are perfectly regular, with the exception of the easternmost station, 1503. The stations in the northern Sargasso group show regular phosphate-temperature relations, excepting certain depths at Station 1481, which lies immediately adjacent to the eastern group of stations. This latter group, on the other hand is highly irregular.

Mean curves for all these groups have been drawn in Figure 28, disregarding those points which fall far outside the envelopes. The result shows close similarity throughout all the Caribbean area, and the same qualitative difference between this and the Sargasso area that was observed in the case of nitrate. Since the mean curve for the eastern group of Sargasso stations is rather arbitrarily drawn it is not safe to compare it too closely with that for the northern group. The principal difference between these two groups of stations is the greater irregularity of the eastern one.

The eastern profile in the Caribbean is for some reason a very special case. The phosphate-temperature relations differ so much from station to station that an average curve would be entirely meaningless. Even the envelope drawn to include the points in Figure 26 is so diffuse as to be little more than roughly indicative.

The reason for the irregular results from this group of stations is not easy to see, although there is other evidence of unusual conditions at the eastern end of the Caribbean basin. The fact that the irregularity extends for a short way up into the Sargasso to the north is perhaps significant.

Turn to page 35

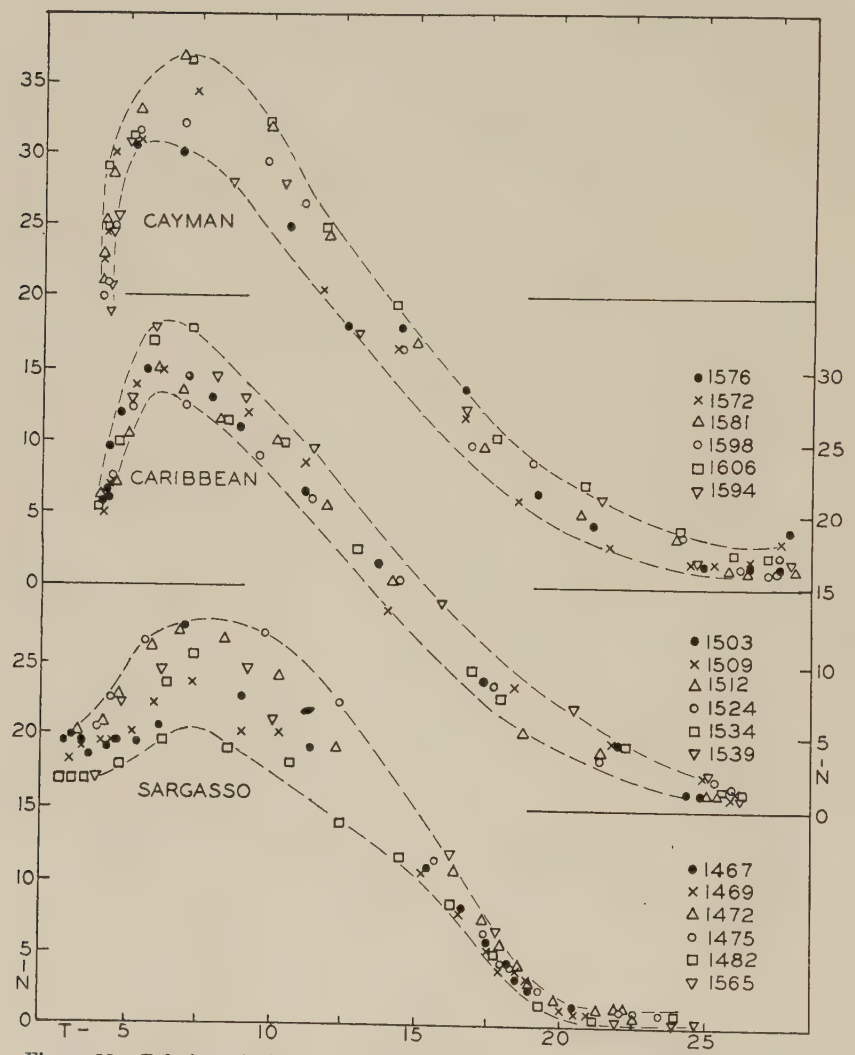

Figure 22. Relation of nitrate to temperature. Stations grouped according to areas. (See Fig. 1.) Broken lines comprise envelopes including points plotted.

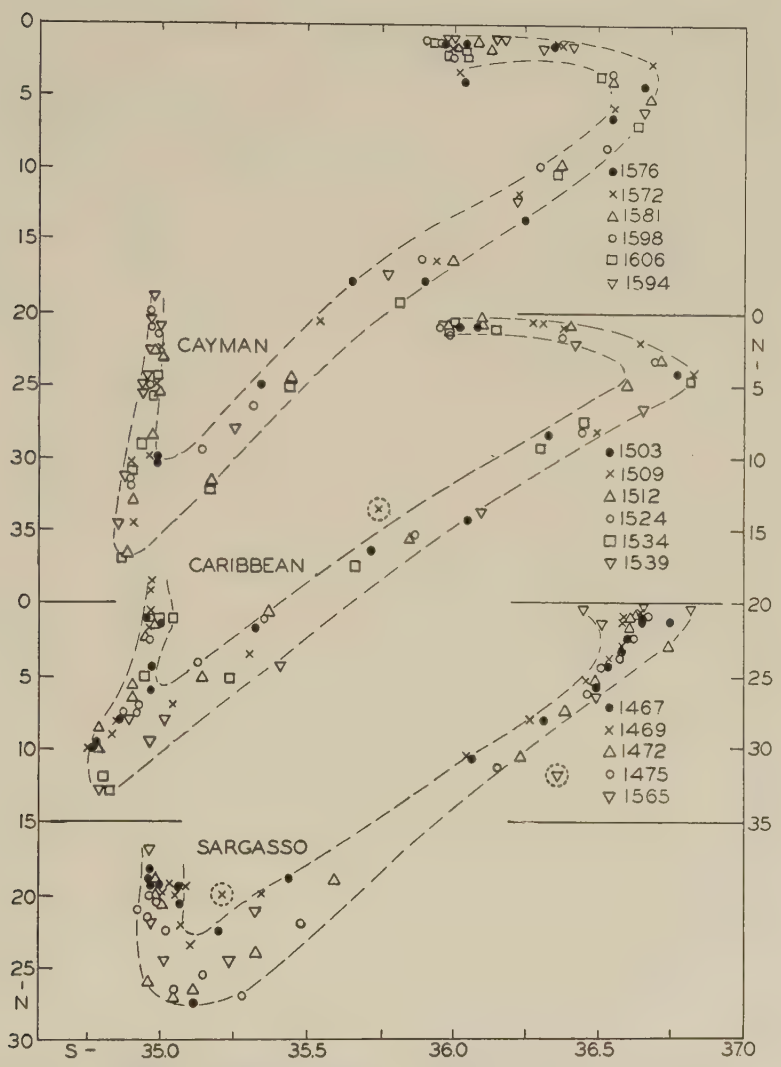

Figure 23. Relation of nitrate to salinity. Stations grouped according to areas. (See Fig. 1.) Broken lines comprise envelopes including points plotted.

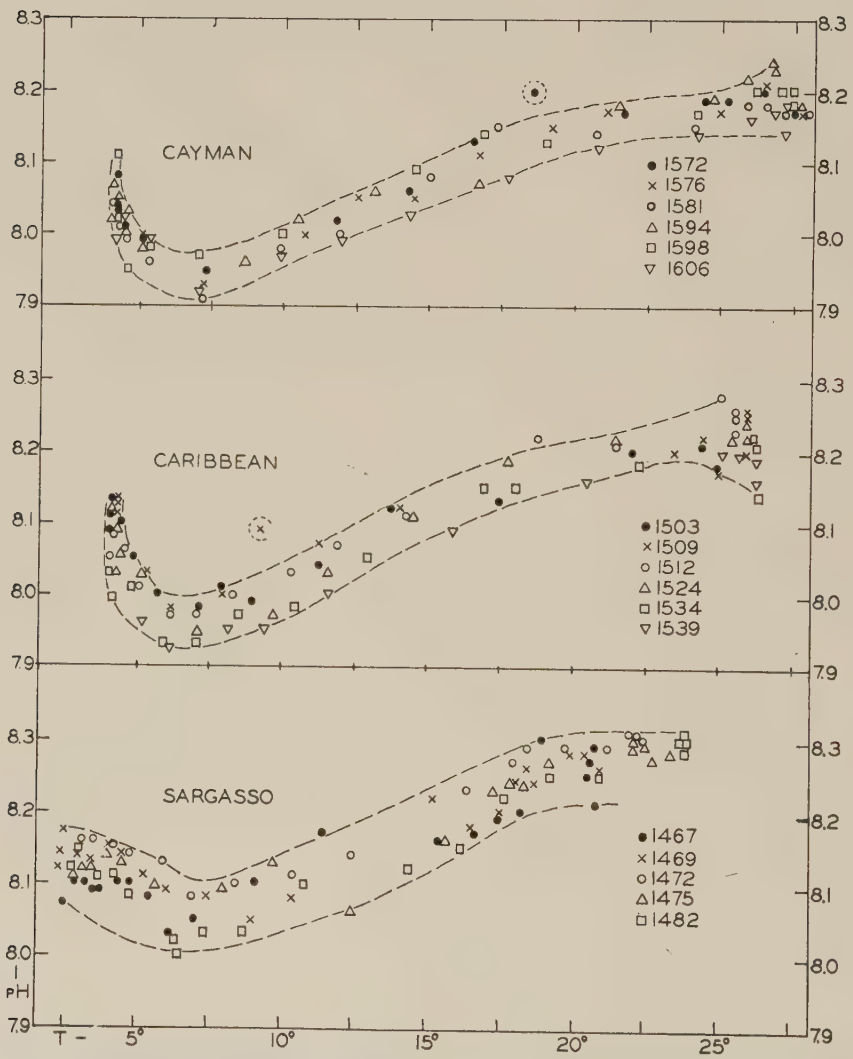

Figure 24. Relation of pH to temperature. Stations grouped according to areas. (See Fig. 1.) Broken lines comprise envelopes including points plotted.

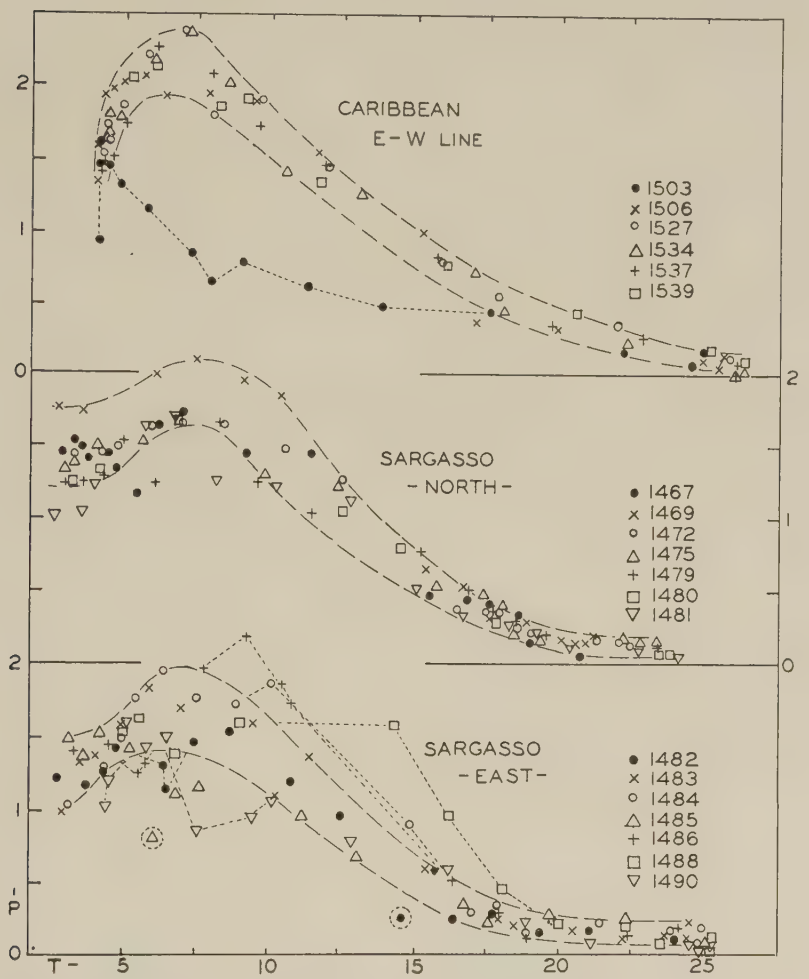

Figure 25. Relation of phosphate to temperature. Stations grouped according to areas. (See text and Fig. 1.) Broken lines comprise envelopes including points plotted, with certain exceptions.

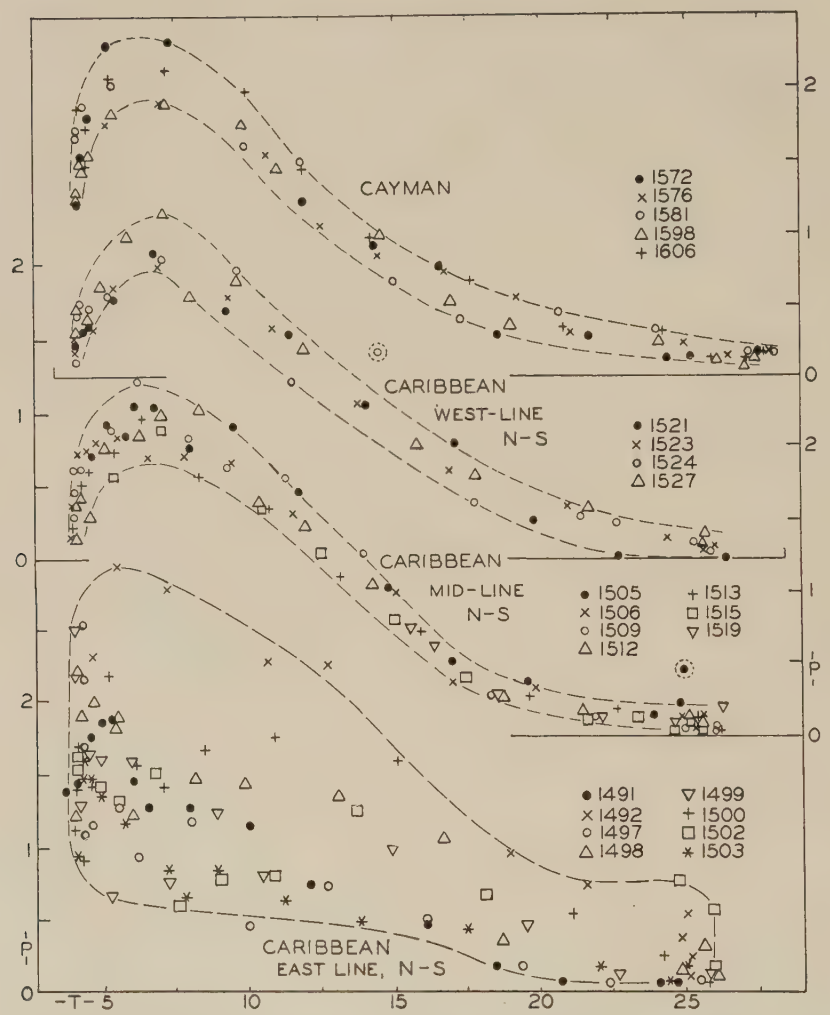

Figure 26. Relation of phosphate to temperature. Stations grouped according to areas. (See text and Fig. 1.) Broken lines comprise envelopes including points plotted, with certain exceptions.

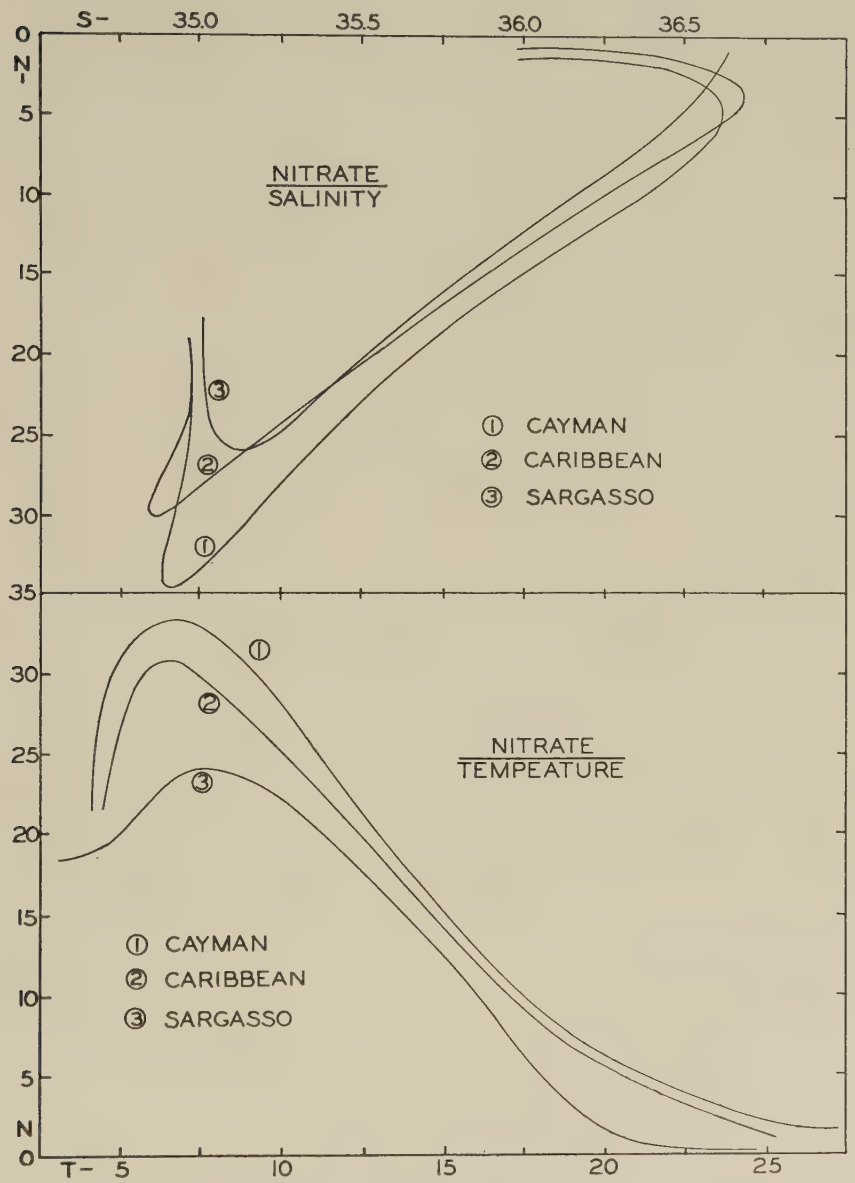

Figure 27. Mean relation of nitrate to temperature and salinity. Mean curves taken from envelopes in Figs. 22 and 23.

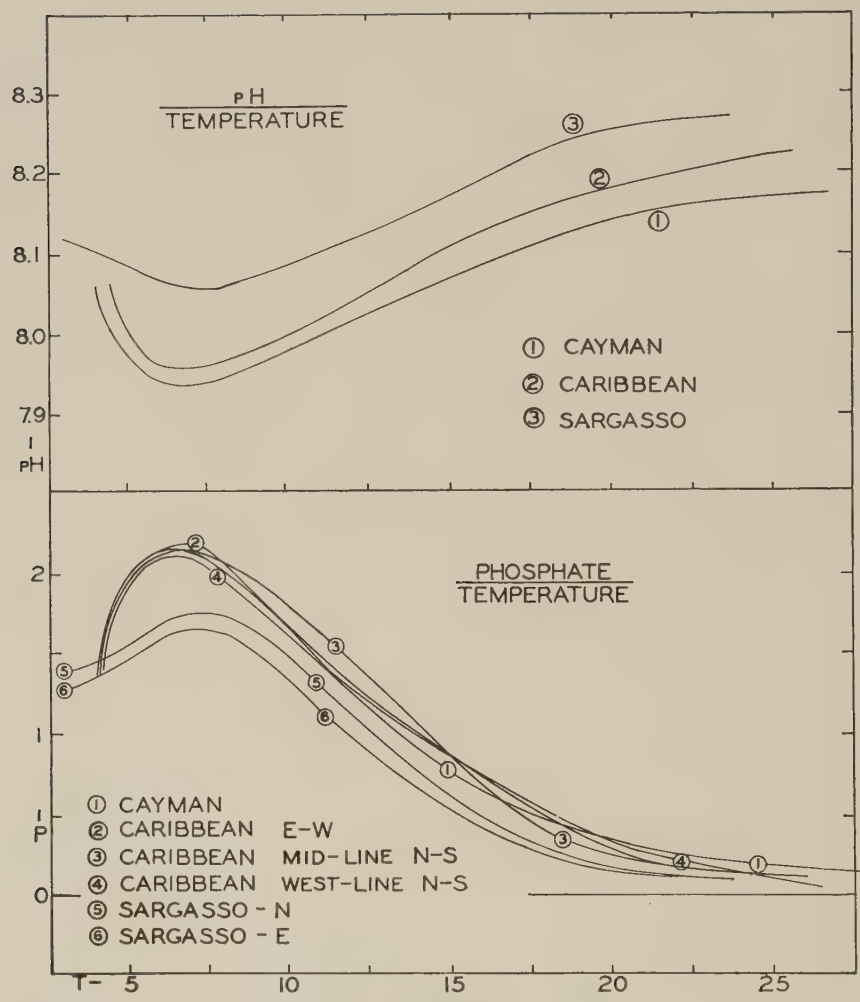

Figure 28. Mean relation of pH and phosphate to temperature. Mean curves taken from envelopes in Figs. 24, 25 and 26.

The vertical distribution of phosphate in the three N-S profiles is shown in the upper portions of Figures 29, 30 and 31. The irregularity of the eastern profile and the regularity of the middle and western ones is again apparent. There are three peculiarities in the eastern profile: the low phosphate concentrations in the south, at all depths; the broadening of the maximum zone in the middle of the profile and its downward displacement, to 2000 meters; a very pronounced maximum at the northern end, rather broad and displaced somewhat towards the surface. In addition to these features there is the irregularity of many individual results at several stations. Contrasted with this, the middle and western profiles are smooth and regular. The only tangible connection with the eastern profile is the broad zone of high concentrations at Stations 1509 and 1527, which seems to be connected with Nos. 1497 and 1499. This is also to be seen in Figure 13.

The eastern profile may be extended north into the Sargasso in an irregular line through Stations 1488 to 1482, as shown in Figure 32. Although this does not help in explaining the unusual phosphate-temperature relations at these stations, it is interesting to observe how this figure fits onto the northern end of Figure 29, even though there is a rather considerable lateral jump between the two lines of stations.

The oxygen profiles for these same groups of stations have been constructed and are given in the lower portions of Figures 29, 30, 31 and 32. The oxygen relations in the eastern profile also show some slight irregularities in the lower depths, as compared with the middle and western ones. The area of highest oxygen concentration, in the lower depths to the southeast, corresponds with low phosphate values.

Comparison of Figures 29 to 32 shows that the oxygen minimum is generally slightly above the phosphate maximum and that the 4.90 contour for oxygen roughly corresponds with the 1.75 for phosphate. In the eastern profile, no relation is found between the oxygen minimum and phosphate maximum, except at the northern end, but 4.90 oxygen corresponds with 1.75 phosphate at Stations 1497 and 1498, although not at 1499.

Unpublished results from two "Carnegie" stations in this same region confirm these findings to a certain extent. One of these stations (No. 31, Cruise 7) nearly corresponds with Station 1499, and the other (No. 32) is mid-way between 1509 and 1512. The methods for determination and calculation of phosphate concentrations were evidently different from those in this work, so that strict comparison cannot be made, but, nevertheless, at 800 meters the phosphate was 25% higher at the western station than at the eastern, which is approximately the same difference as that between these two profiles.

It is unfortunate that the data for nitrate are too limited to confirm those for phosphate. Only at Stations 1497 and 1503 were nitrate analyses made, and in neither case was any particular irregularity noted.

It does not appear possible to explain the three main features of the eastern line by means of any simple picture of circulation or mixing of water masses. A certain degree of abnormality in this profile was found by Parr (*1*). The relatively shallow passages between the Lesser Antilles constitute a threshold between the Atlantic and Caribbean, and it is suggested that some of the bottom water of the latter has its source in the process of "cascading" over this threshold, as a result of the rise and fall of the lower levels outside. The low phosphate and high oxygen in the deeper water at the southern end of the profile do indeed have their counterparts in the equatorial waters to the southeast. The oxygen values reported from two of the "Dana" stations, near Barbados and further to the east, correspond closely to those at Stations 1499, 1500 and 1501. The phosphate at Stations 1501, 1502 and 1503 is similar in amount to the values cited by Seiwell (*12*) for waters to the southeast.

While such a picture might help us to understand the southern end of this profile it offers no explanation for the high phosphate in the central and northern parts. The source of phosphate, as well as the explanation of the other irregularities, must be sought within the water itself.

This should cause us no great concern, for the same is true—although perhaps to a less extent—throughout the water of the Caribbean area. Neither phosphate nor the nitrate can be accounted for in terms of the inflowing water.

Their concentration in the water is the result of the nature and state of the biological activity within it. Constancy of the P/T ratio, for example, is dependent upon a uniform biological environment; variation may result from local differences in this environment, as well as from mixture with water of a different source. The explanation of the distribution of nitrate and phosphate and their apparent rise and fall across an area like this involves the mechanism of the cycle of decomposition and regeneration of organic and nutrient matter. Although some of the general features of this cycle are known, the explanation of the picture observed at any one point necessitates more information that these data yield. The distribution of plankton in a given area, the effect of adjacent rivers (such as the Orinoco near the location under discussion above), unknown factors which may determine the rate of hydrolysis and oxidation of organic phosphorus and nitrogen compounds—all these are considerations which may well be important but which have necessarily been left out of account.

Our present results indicate a peculiar biological environment in this region. Whether this is true in general, or only a temporary phenomenon at the time it was visited, there is no indication. It would seem well worth further study.

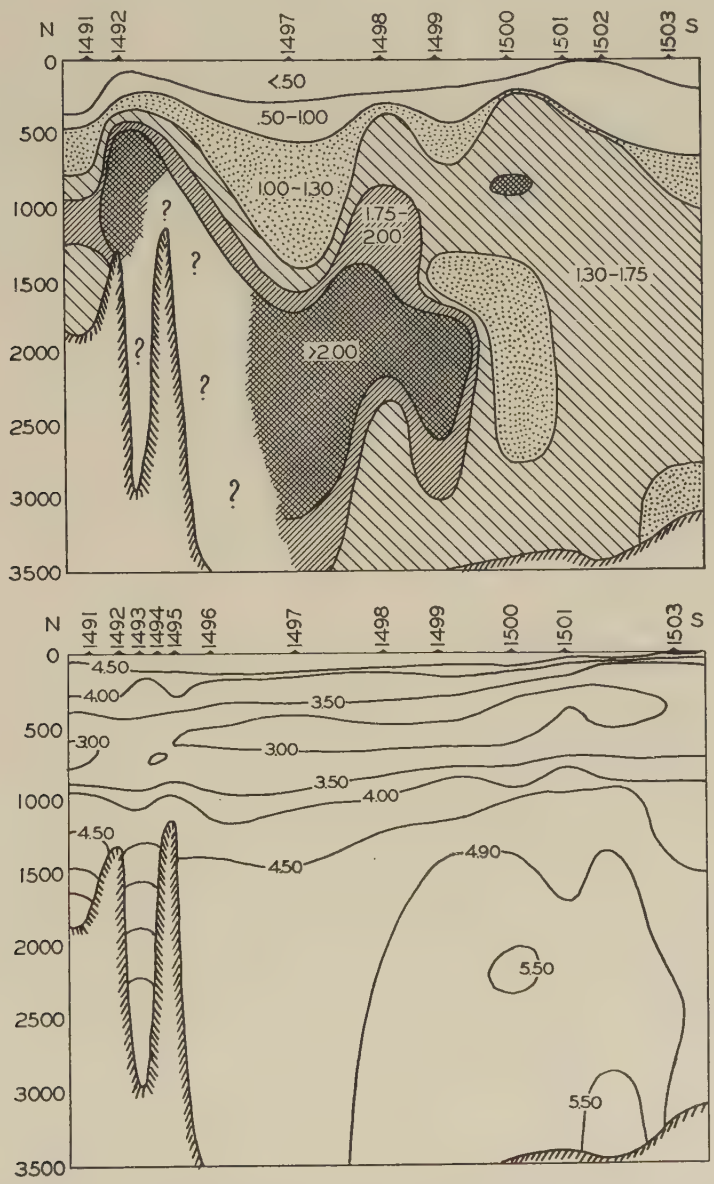

Figure 29. *Above:* Phosphate in the East Line of the Caribbean. *Below:* Oxygen. Depths vertically in meters. Phosphate units, milligram atoms per liter. Oxygen units, ml. per liter.

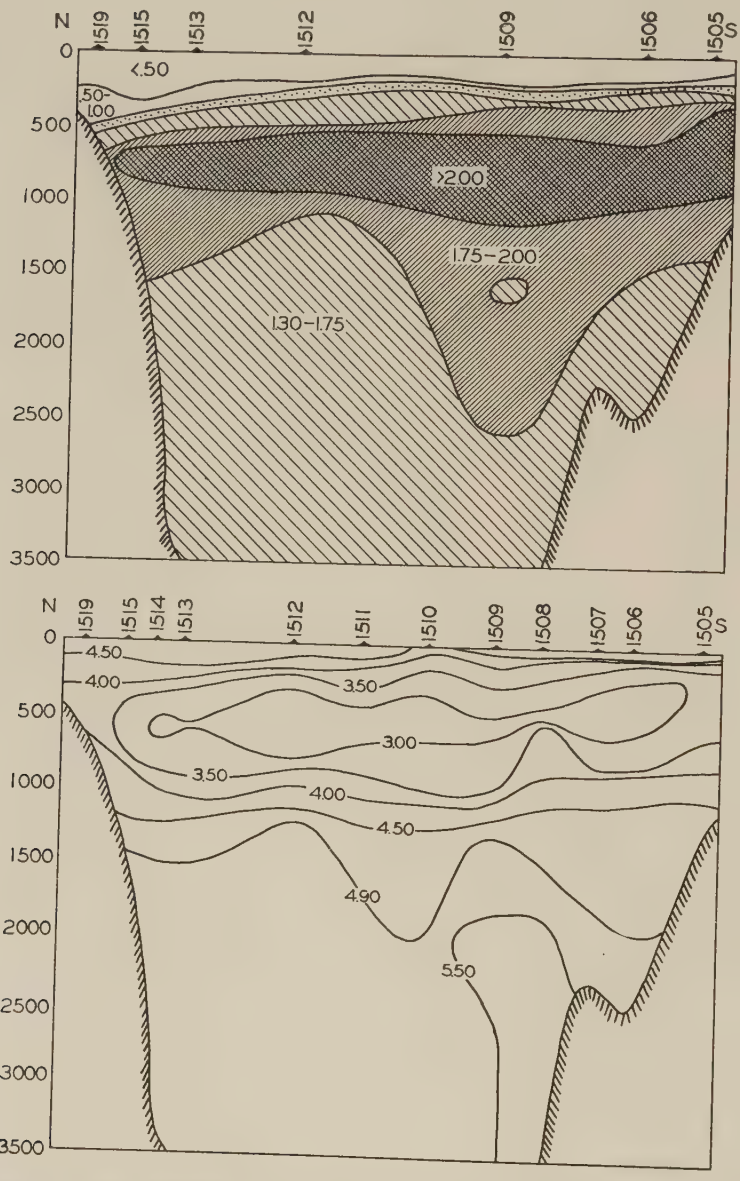

Figure 30. *Above:* Phosphate in the Mid-Line of the Caribbean. *Below:* Oxygen. Depths vertically in meters. Phosphate units, milligram atoms per liter. Oxygen units, ml. per liter.

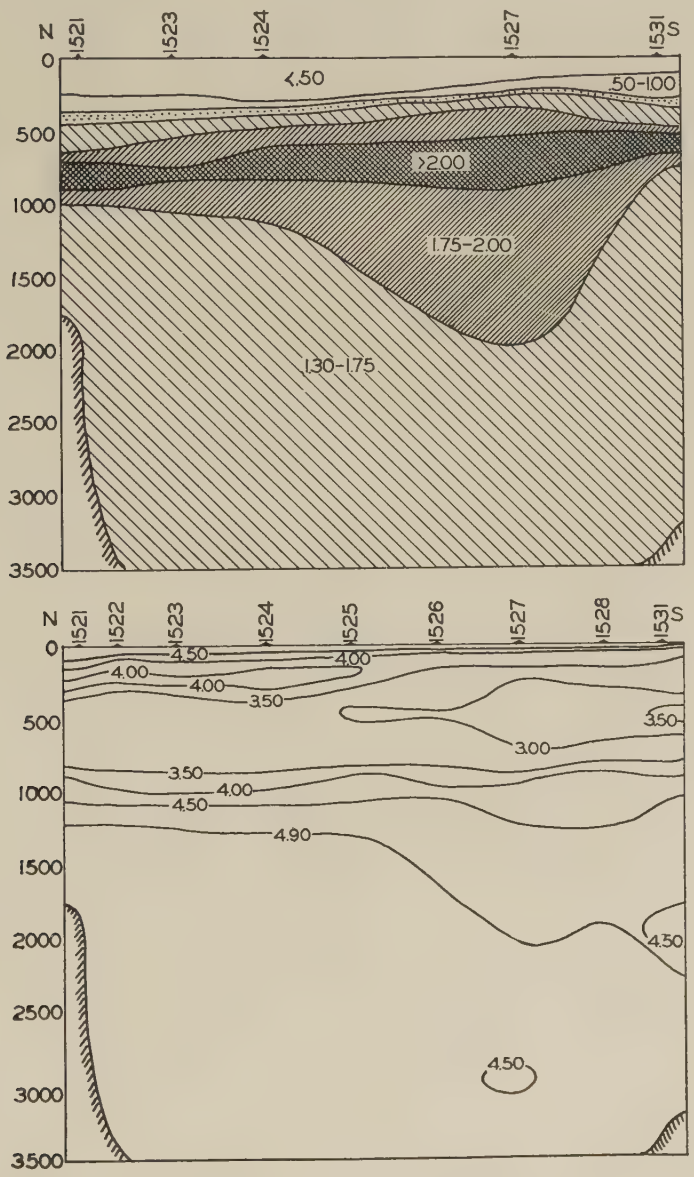

Figure 31. *Above:* Phosphate in the West Line of the Caribbean. *Below:* Oxygen. Depths vertically in meters. Phosphate units, milligram atoms per liter. Oxygen units, ml. per liter.

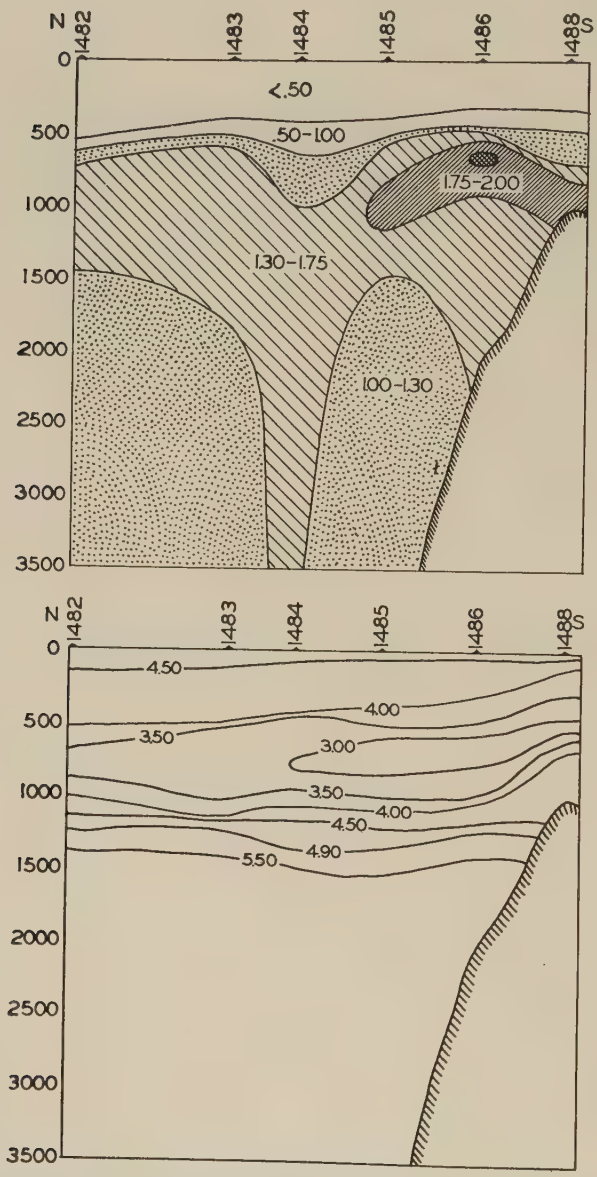

Figure 32. *Above:* Phosphate in the Sargasso (East Group). *Below:* Oxygen. Depths vertically in meters. Phosphate units, milligram atoms per liter. Oxygen units, ml. per liter.

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The Determination of Dissolved Nitrogen in Water

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IN THE COURSE of the study of sea water it became necessary to make determinations of its nitrogen content. Earlier measurements were not explicit on the separation of the argon and other inert gases, and a method was accordingly sought which would yield values for nitrogen directly, rather than by difference. It was essential that the analysis be fairly rapid, to permit the routine determination of as many samples as possible, and accurate to about 1 per cent of the nitrogen present, and that it require not more than about 100 ml. of water.

The procedure to be described consists of two definite parts: removal of the total gas from the water sample, and its analysis for nitrogen. The first step is accomplished by repeatedly spraying the water into an evacuated chamber, removing the extracted gas after each injection. The quantity of extracted gas is measured manometrically in a constant volume, and its content of oxygen and nitrogen, respectively, measured in the same way after reaction with phosphorus and with lithium. Calcium, magnesium, and lithium have all been used as reagents for combination with free nitrogen, but preliminary work showed that lithium was the most suitable under the conditions necessary for this work.

Description of Apparatus

Figure 1 shows the necessary working parts of the apparatus, with a slight exaggeration of scale for the smaller parts. It is constructed entirely of Pyrex glass, although soft glass may of course be substituted for the long manometer arms. All connections are made of 7-mm. tubing, and the section in which the analysis is carried out, between *a*, *b*, *d*, and *f*, is of 7-mm. capillary, to reduce the volume.

The mercury reservoir, *D*, which serves as a pump, has a volume of 250 ml. The evacuation chamber, *E*, in which the gas is extracted, has a volume of 300 ml., and connects with a large mercury leveling bulb, as shown. Chamber *F*, in which the water sample is measured and stored, has a capacity of 100 ml.

Ground-glass joints occur at *a*, *f*, *g*, and *b*, and the latter, which is not lubricated, is protected with a mercury seal held in place by a short piece of rubber tubing.

The phosphorus chamber, *A*, has a volume of between 2 and 3 ml. with a small plug of glass wool. The lithium chamber, *B*, has a similar volume and contains a deep steel crucible made by drilling out a steel rod. The chamber is surrounded with an asbestos shield.

The tip of the jet, *h*, where it enters *E*, is drawn down to about 0.5 mm. This orifice should be as small as possible, without

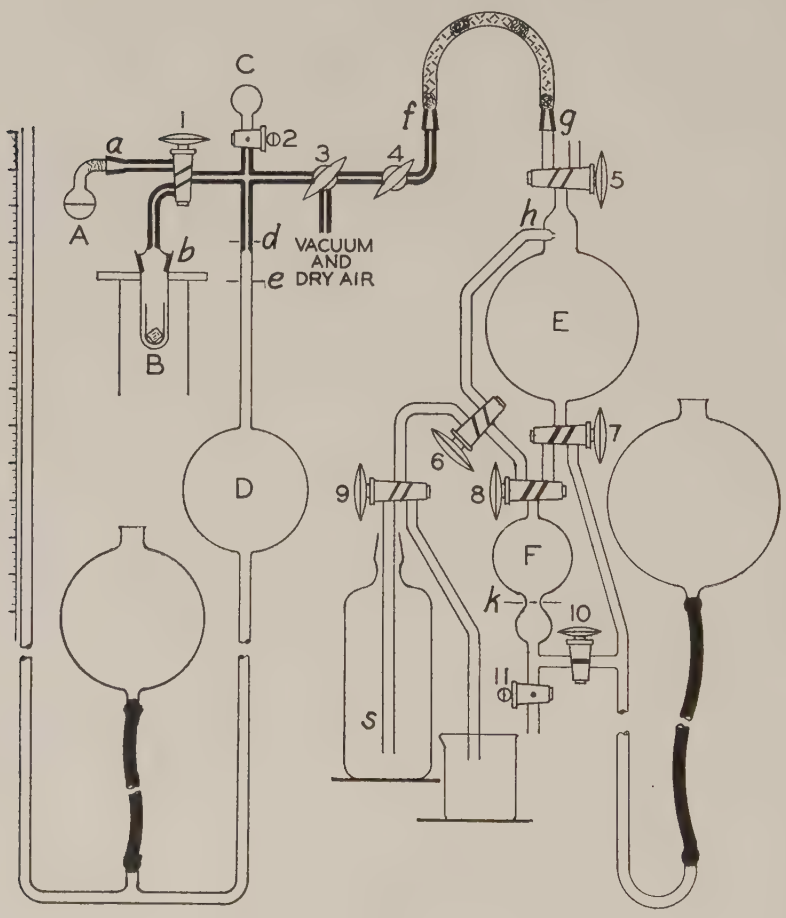

FIGURE 1. DIAGRAM OF APPARATUS

danger of clogging. The water enters *E* through this orifice, at high velocity.

The inverted U-tube contains ascarite, calcium chloride, and dehydrite, in that order, separated by plugs of cotton, for the purpose of removing carbon dioxide and water vapor from the extracted gas. It is made of 8-mm. tubing, about 20 cm. from *f* to *g*. It can be removed from the line at the ground-glass joints for refilling, and short lengths of glass rod are inserted in the male parts of these joints, to reduce the volume.

The volumes of chamber *C* and stopcock 2 are determined before sealing them into the line, and should lie between 1.5 and 2 ml., approximately the volume of the sample to be analyzed.

The analytical part of the apparatus as far as stopcock 5 is evacuated by means of a Hy-vac pump, and the suction line contains a 3-way stopcock (not shown) through which dry air can be admitted to the system through calcium chloride and soda lime.

The mercury used in *D* should be dried in an oven occasionally, and the manometer evacuated to remove moisture.

Manipulation

Preparation of Phosphorus. After filling the phosphorus chamber with pieces cut under water, and plugging the end with glass wool, the moisture must be removed by heating and evacuation, being careful that bubbles do not carry phosphorus out of the tube. The removal of water is complete when the pressure in the system is constant on heating and cooling.

Preparation of Lithium. Bright pieces of lithium are cut under dry carbon tetrachloride and placed in the steel crucible and the chamber is closed and evacuated as rapidly as possible. After evacuation the lithium is melted to drive off all volatile matter. It was found that the first heating of fresh lithium liberated some volatile products, most of which recombined with the metal on continued heating. The noncombined residue is then pumped off, after which repeated heating and cooling produce no further changes in pressure. The nature of this phenomenon was not further investigated, but it was observed that subsequent reaction of the lithium and nitrogen proceeded more rapidly if only the noncombining residue was pumped off. Lithium from which all the volatile substances were removed during heating was very slow to react with nitrogen the first two or three times, but its reactivity increased thereafter.

The lithium prepared in this way can be used for as many as ten analyses.

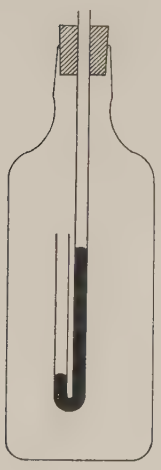

Figure 2

Calibration of Volume. A reference mark is established at *e*, about 1 cm. below the end of the capillary tubing, and all pressure and volume measurements are made with the mercury at this mark. The gas being measured is in every case contained in *C* and in the rest of the system between 1, 3, and *e*. The volume of *C* being known accurately, this quantity of dry air can be introduced into the system and the pressure read on the manometer. The difference between this reading and that of the evacuated system calibrates the manometer for subsequent readings, subject, of course, to changes in atmospheric conditions.

Measurement of Water Sample. The water sample is measured in *F*, between stopcock 6 and a reference mark, *k*. Chamber *F* and the inlet connections around to the end of tube *s* are first filled with mercury and the sample is sucked in slowly from the original bottle. The volume contained in this chamber is calibrated by the weight of water removed from a sample. For this particular apparatus it was 101 ml.

Gas Extraction

It is convenient to arrange three supports for the main mercury leveling bulb: one at the level of 5, another at the level of 10, and another about 80 cm. below 10.

The water sample is sucked into F as described above. Chamber E is evacuated by filling with mercury and lowering. Raising the mercury bulb, the water is forced from F into E, by both suction and pressure. This is continued until mercury comes through h. As the water issues from the orifice at high velocity and strikes the neck of the flask, the greater portion of the dissolved gas is removed from solution. The water sample is run down into F again, through 7 and 8. Mercury is then run up into E, through 7, and the extracted gas is forced into the drying tube, which in the meantime has been evacuated by the oil pump, along with the remainder of the analytical line. There will always be a few drops of water on the surface of the mercury and a little of this must be run up into the stopcock and later removed very carefully by suction.

Chamber E is then evacuated by lowering the mercury and the water sample again injected through 8, 6, and h. The small amount of gas extracted in this stage is also forced into the drying tube. Four such circulations of the water, or at most five, will remove all but insignificant amounts of dissolved gas. The first stage is always somewhat slower than the subsequent ones, because of air bubbles.

Analysis of Gas

After reading the manometer with the analytical line evacuated, stopcock 1 is closed, 3 and 4 are opened, and the mercury is lowered in D, whereby most of the extracted gas is removed from the drying tube. Stopcocks 3 and 4 are closed and the gas is forced into C. Stopcock 2 is then closed and the remaining gas in the drying tube is pumped into D by lowering the mercury again. This is also forced into C, leaving only an insignificant residue in the drying tube. Opening 2, the volume of total gas is measured manometrically between 1, 3, and e.

By means of the mercury in D the gas is pumped out of C into A. The phosphorus is melted by gentle heating and allowed to react for 5 minutes, after which the remaining gas is pumped out of A into D and then back again, where it is allowed to react with the melted phosphorus for a few minutes longer.

The deoxygenated gas is pumped back again into C, in two stages as before, and its volume measured manometrically. In the same way, it is then pumped in two stages into the lithium chamber, B. The lithium is heated above its melting point. This can be done electrically, but it was found more convenient to use a Bunsen burner. As combination of the nitrogen with the lithium goes on it is necessary to lower the mercury level continually, to keep the inside level approximately at d. The reaction is generally completed in 5 minutes.

After cooling, the residue is pumped into C again and its volume is measured by the manometer. From the four pressure readings and the laboratory temperature and pressure it is possible to calculate the total volume of gas dissolved per liter of water and the relative and absolute amounts of oxygen and nitrogen in the gas.

The entire process of extraction and analysis requires about an hour and a quarter, but the actual time may be considerably shortened by carrying out the analysis of one sample and the extraction of the next simultaneously. The drying tube may be evacuated and closed off ready for the next sample as soon as the preceding one has been pumped out of it.

Accuracy of the Method

Attempts were made to check the accuracy of the method by comparing the volumes of gas extracted from air-saturated

distilled water with accepted values. Water was shaken with air in a flask for 15 minutes and then allowed to stand open in the laboratory for several days. The volumes of air extracted from such water samples and the accepted values for the solubility of air are given in Table I. Uncertainty as to the degree of saturation of the water may partially account for the fact that the observed results were about 1 per cent below the theoretical. Nevertheless, this percentage of error is not considered unreasonable.

The completeness with which oxygen is removed by this method was checked by comparing the values obtained for oxygen in samples of sea water against the results obtained simultaneously by the standard Winkler method. Table II shows this comparison. Only in the last case is the discrepancy significantly beyond the limits of error of the two methods.

TABLE I. DETERMINATION OF DISSOLVED AIR

Temp.	Dissolved Air	
	Observed	Theoretical
° C.	*Ml./l.*	
24.3	17.3	17.5
22.0	18.0	18.0
22.0	17.8	18.0
22.0	17.8	18.0
23.0	17.3	17.7
Av.	17.6	17.8

TABLE II. REMOVAL OF OXYGEN

O_2 by Extraction	O_2 by Winkler	O_2 by Extraction	O_2 by Winkler
Ml./l.	*Ml./l.*	*Ml./l.*	*Ml./l.*
4.45	4.46	4.31	4.28
4.85	4.89	5.12	5.12
5.01	4.94	5.15	5.20
4.60	4.52	5.42	5.54
4.76	4.71	Av. 4.85	4.85

TABLE III. ANALYSIS OF AIR

O_2	N_2		O_2	N_2	
%	%		%	%	
20.7	77.7		20.9	....	
20.7	78.1		20.8	78.1	
20.9	77.8		21.1	78.1	
21.1	77.1	Av.	20.8	77.9	
20.6	....				
20.6	78.3	Theoretical	20.99	78.03	(Critical Tables)

Samples of air were analyzed for oxygen and nitrogen, further to check the accuracy of the method. This was done by filling chamber *C* with air passed through calcium chloride and soda lime. The volume of this sample, 1.52 ml., is approximately that obtained from 100 ml. of sea water. Table III shows the results, compared with values from International Critical Tables.

Storage of Water Samples

Since the apparatus was not adapted for use on board ship, it was necessary to store the water samples taken at sea

in such a way as to prevent interchange of gas between the water and the atmosphere. It is impossible to keep samples in the ordinary type of citrate bottle, tightly clamped with no cushion of air over the water, without a large percentage of breakage. This difficulty was completely overcome by the device shown in Figure 2, which consists of a U-tube partially filled with mercury and inserted in a citrate bottle completely filled with water. Expansion and contraction merely move the mercury column, and although water may escape outward past the mercury none passes the other way. When inserting the tube care must be taken that water completely fills the short arm and that no air is trapped by the stopper. Samples are stored in a refrigerator until analyzed, especially the deeper, colder samples, which may become supersaturated at higher temperatures.

Analyses

To show the results of the application of the method to actual sea water some analyses are given in Table IV. These samples are from various depths at two different stations in

TABLE IV. ANALYSES OF SEA WATER

Station 2666			Station 2667		
Depth	Temp.	Nitrogen	Depth	Temp.	Nitrogen
Meters	° *C.*	*Ml./l.*	*Meters*	° *C.*	*Ml./l.*
0	25	9.72	....	....	.....
10	22.5	9.50	10	26.0	8.83
40	14.3	11.0	....	....	.....
60	12.5	11.0	60	20.9	9.67
80	12.0	10.8	....	....	.....
100	12.3	11.1	....	....	.....
150	7.9	11.4	....	....	.....
200	9.6	11.7	200	18.2	9.64
300	7.7	12.4	....	....	.....
400	5.2	12.6	....	....	.....
500	4.7	12.7	500	17.3	10.3
600	4.7	12.5	....	....	.....
800	5.2	12.6	800	14.8	10.4
1000	4.0	12.5	1000	11.5	11.3
1200	4.1	12.8	....	....	.....
1500	3.6	12.8	1500	5.2	12.6
2000	3.5	13.0	....	....	.....
3000	2.6	13.3	....	....	.....
....	...	....	4000	3.1	13.9

the Atlantic south of Cape Cod: No. 2666, north of the Gulf Stream; and No. 2667, south of the Gulf Stream. Further studies on the content of dissolved nitrogen in sea water will be reported in a subsequent paper.

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SHORT-PERIOD VARIATIONS OF OCEANOGRAPHIC CHARACTERISTICS IN THE WESTERN NORTH ATLANTIC

H. R. Seiwell

(Contribution No. 142 of the Woods Hole Oceanographic Institution)

The existence of short-period variations of oceanographic characteristics at fixed levels in the oceanic basins has been demonstrated by various investigators (Björn Helland-Hansen and Fridtjof Nansen, The eastern North Atlantic, Geofysiske Publikasjoner, v. 4, No. 2, 1926, 71 pages; Björn Helland-Hansen, Report of the scientific results of the Michael Sars North Atlantic deep-sea expedition 1910--Physical oceanography and meteorology, Part 1 (text), 1930, 115 pages; Albert Defant, Die Gezeiten und inneren Gezeitenwellen des Atlantischen Ozeans, Wiss. Ergeb. Deutschen Atlant. Exped. Meteor 1925-1927, v. 7, Part 1, 1932, 318 pages). But since such information is scanty, a study of the question in the western North Atlantic was begun with the establishment of Station 2639 (66° 25' west, 35° 07' north) by the Atlantis July 9 to 13, 1936. (For details of the operation of this Station and complete discussion of the results, see H. R. Seiwell, Short-period vertical oscillations in the western basin of the North Atlantic, Papers Phys. Oceanogr. and Met., v. 5, No. 2, in press.)

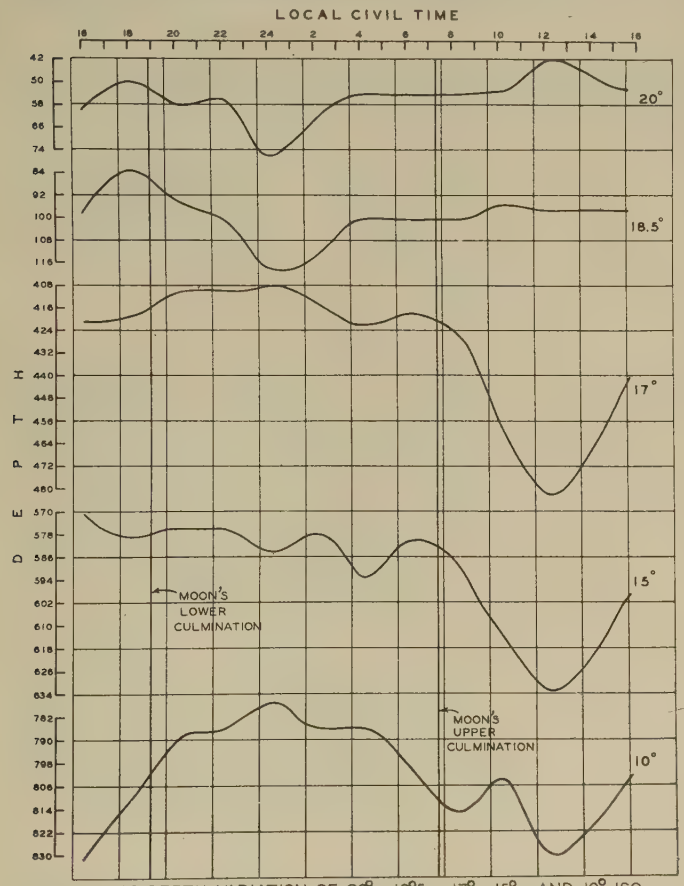

FIG. 1—TIME-DEPTH VARIATION OF 20°-, 18°.5-, 17°-, 15°-, AND 10°-ISOTHERMS, ATLANTIS STATION 2639, 24-HOUR PERIOD BEGINNING 15^h30^m, JULY 12, 1936

The present discussion is confined chiefly to the results of a series of approximate two-hour samplings of the upper 1200 meters of the water-column at Station 2639 during the 24-hour period beginning $15^h\ 34^m$, July 12, 1936. The observed vertical range of the isotherms for 20°, 18°.5, 17°, 10°, and 5° are given in Table 1 and their depth-time variations are illustrated in Figure 1, possible connections with the tidal wave being suggested by the appearance of approximate 12- and 24-hour periods.

Table 1

Isotherm	Mean depth	Total depth-range
	meters	meters
20.0	60	42 - 76
18.5	101	83 - 118
17.0	428	408 - 482
15.0	591	571 - 633
10.0	816	777 - 830
5.0	1265	1242 - 1285

Vertical variations of isotherms (and other characteristics in the sea) may be produced either by horizontal or vertical shifts of the water-mass. However, a detailed study of the horizontal gradients of the 17° and 10° isotherms in the vicinity of Station 2639 revealed that the minimum horizontal velocities (at the respective mean depths of these isotherms) required to produce the observed vertical displacements of isotherms would need to be in excess of 100 to 200 cm per second; such values are considered outside the realm of probability. Hence, it seemed reasonable to conclude that the observed variations of temperature and other oceanographic characteristics at Station 2639 resulted primarily from vertical oscillations of the water-column rather than from horizontal displacement of the water-layers.

Harmonic analysis of depth-variations of the 20°, 17°, and 10° isotherms (for the 24-hour period beginning $15^h\ 34^m$, July 12) gave the following results:

$$H_{20°} = 55.4 + 7.4 \cos (2\pi/24)\ (t - 5^h.2) + 1.8 \cos (2\pi/12)\ (t - 5^h.8) + 5.6 \cos (2\pi/8)\ (t - 5^h.2)$$
$$H_{17°} = 430.4 + 27.5 \cos (2\pi/24)\ (t - 16^h.6) + 14.0 \cos (2\pi/12)\ (t - 5^h.2) + 9.4 \cos (2\pi/8)\ (t - 0^h.9)$$
$$H_{10°} = 802.4 + 24.7 \cos (2\pi/24)\ (t - 17^h.4) + 4.1 \cos (2\pi/12)\ (t + 1^h.6) + 2.3 \cos (2\pi/8)\ (t - 6^h.4)$$

where t stands for the number of lunar hours after the moon's lower culmination on July 12.

Good convergence is obtained between values calculated by means of the above equations and the observational data; the close agreement of calculated and observed extreme positions for the 20°, 17°, and 10° isotherms during the 24-hour period beginning $15^h\ 34^m$, July 12, is illustrated by Table 2.

Table 2--Comparison of calculated and observed extreme isotherm-positions
(Figures in parentheses represent the approximate number of lunar hours after the lower culmination of the moon on July 12, 1936)

Isotherm	Calculated range	Maximum displacement	Observed range	Maximum displacement	Average deviation all values
°	meters	meters	meters	meters	meters
20	44.1 (17^h) - 70.0 (5^h)	25.9	42 (17^h) - 76 (5^h)	34	2.2
17	407.5 (4^h) - 481.1 (10^h)	73.6	408 (5^h) - 482 (17^h)	74	1.9
10	774.7 (4^h) - 822.3 (16^h)	47.6	777 (5^h) - 830 (17^h)	53	5.3

Considering the depth-variations of the isotherms examined (as shown by the previous equations), the effect of the 24-lunar-hour wave was most pronounced, its amplitude attained significant proportions in the principal thermocline layer (24.7 to 27.5 meters), and its phase increased with increasing depth. The 12-lunar-hour wave was less effective, and had an amplitude of 20 to 50 per cent of that of the 24-lunar-hour wave (4 to 14 meters in the thermocline). The 8-lunar-hour wave showed its greatest relative significance at the depth of the 20° isotherm where its amplitude (5.6 meters) was more than three times that of the 12-lunar-hour wave (1.81 meters), but reached its maximum amplitude (9.4 meters) at the depth of the 17° isotherm where it was relatively less important. It may be concluded tentatively that the 24-lunar-hour and 12-lunar-hour waves are connected with the diurnal and semidiurnal tidal waves, but no tidal significance, as far as is known, can be attached to an 8-lunar-hour wave.

The question now naturally arises as to the effect of vertical oscillations of the water-column on the significance of conclusions derived from the usual oceanographic investigations (for example, from a study of temperature-, salinity-, and oxygen-distribution at fixed levels in the sea). The present study is not based on sufficient data to warrant the use of the results to approximate the effect of vertical oscillations at Station 2639 beyond the time of observation, but it is possible from the standpoint of practical oceanography to ascertain the order of magnitude of variations which, in general, may be expected to take place at fixed levels in the sea, from which can further be demonstrated the degree of disparity to be expected in various oceanographic calculations on account of the existence of vertical oscillations.

Thus, considering the temperature-variations, the calculation of the values $(t°_{max} - t°_{min})$ for a series of fixed levels between the surface and 5000 meters (based on data obtained during the entire observational period of 4 1/4 days at Station 2639) gave the following results: At the surface the maximum temperature-difference was 0°.30; but at 50 meters, which laid in the summer thermocline, it had increased to 2°.66; and below, in the relatively homogeneous water, between 200 and 400 meters, variations of only 0°.31 to 0°.36 were obtained. On entering the principal thermocline, which approximately laid between 400 and 1200 meters, the variations in $(t°_{max} - t°_{min})$ again became great, increasing from 0°.90 at depth 500 meters to a maximum value of 1°.42 at depth 800 meters and then falling off continuously to 0°.79 at depth 1100 meters and to 0°.50 at depth 1200 meters. In still deeper water, below the thermocline, values of $(t°_{max} - t°_{min})$ continued to decrease with decreasing vertical temperature-gradient; between 1400 and 2000 meters the values declined from 0°.36 to 0°.09 and continued to diminish still deeper until at depth 5000 meters the value of $(t°_{max} - t°_{min})$ was 0°.02--the approximate error of the thermometers.

A similar variation was observed in the case of oxygen. Values of $(O_{2_{max}} - O_{2_{min}})$ greater than 0.15 cc per liter occurred in the upper 2250 meters--with maximum values, 0.30 to 0.60 cc

per liter, coinciding with the maximum vertical oxygen-gradient, between 50 and 200 meters. For still deeper water the value of ($O_{2_{max}} - O_{2_{min}}$) decreased, coinciding with the decreased oxygen-gradient, but this value was never less than 0.07 cc per liter for any particular fixed level.

The short-period variations of oceanographic characteristics at fixed levels may cause significant discrepancies in calculations of the dynamic topography, current-velocities, water-transports, and similar results in the sea. Thus, two calculations of the anomaly of dynamic height based on two separate samplings of the water-column at Station 2639 (series C, $22^h\ 27^m$, July 9, to $2^h\ 00^m$, July 10; series H, $13^h\ 35^m$ to $17^h\ 18^m$, July 11, LMT) showed a discrepancy, with reference to 2000 meters, of 8.45 dynamic centimeters; this is sufficient (at the latitude of Station 2639) to produce an error of 25.3 cm per second in the calculated horizontal current-velocities normal to two verticals in the sea separated by a distance of 40 km.

A numerical example of the effect of vertical oscillations at Station Atlantis 2639 on calculations of the transport of water between two verticals in the sea may be obtained by comparing the transport as calculated between series C of Station 2639 and Station 1226 by the Atlantis (35° 07' north, 71° 53' west) with the value obtained from a similar calculation between series H of Station 2639 and Station 1226 (these total transport-calculations were carried out by the method of W. Werenskiold; see Coastal currents, Geofysiske Publikasjoner, v. 10, No. 13, 1935, 14 pages). Thus, the following results of the two transport-calculations between surface and a 2000-meter reference-level were obtained:

Total transport calculated between series C of Station 2639 and Station 1226 . . . 64×10^{11} cm^3 per second

Total transport calculated between series H of Station 2639 and Station 1226 . . . 19×10^{11} cm^3 per second

These results, which illustrate the order of magnitude of the disparity which may arise in a calculation of the total transport of water between two verticals in the sea on account of vertical oscillations of the water-column, are somewhat startling in view of the fact that under the usual methods of oceanographic sampling either series C or H might have been considered representative of Station 2639. The percental difference amounts to $(64 \times 10^{11} - 19 \times 10^{11})/(64 \times 10^{11}) = 70.3$ per cent.

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CURRENT-MEASUREMENTS IN THE GEORGES BANK CANYONS

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(Contribution No. 143 of the Woods Hole Oceanographic Institution)

Among the many speculations concerning the origin of submarine canyons, bottom-currents of various types have been appealed to frequently. This is one theory to which it is possible to apply some quantitative data, and to form an estimate as to the importance which may be attached to this means of producing submarine canyons, both now and in past ages. I refer of course to normal currents due to differences in densities caused by temperature and salinity, and to those which have a tidal origin, and not to the type recently proposed by Daly. Consequently during the summer of 1936 measurements of the bottom-currents were made in three of the submarine canyons of Georges Bank from the research vessel Atlantis of the Woods Hole Oceanographic Institution. Because of the physical difficulties of obtaining readings on the bottom in deep water, in a region where tidal currents at the surface are strong, the results are far from giving a complete picture. Nevertheless, some idea may be obtained of the magnitude of the velocities which might be expected.

The instrument used was an Ekman meter which is too well known to warrant detailed description here. For an account of its construction, one should refer to V. W. Ekman's publication (An improved type of current-meter, Conseil Perm. Internat. J. Conseil, v. 7, pp. 3-10, 1932). Velocities are measured by recording the turns of a delicately balanced propeller, and a device controlled by a compass-needle gives the direction of the current. The instrument is designed to be suspended from a wire, and when it has been lowered to the desired depth the propeller is released by means of a messenger which is slid down the wire. It is stopped in the same manner by another. Consequently, only the current at a given level is recorded and the machine does not register during lowering or raising. Due to the motion of the ship and the inevitable wire-angle, it is impossible to get readings close to the bottom in deep water by the usual procedure of lowering the meter on a wire. The instrument, therefore, was suspended in a framework of brass pipe fitted with a device for releasing one messenger when the frame touched the bottom, and another when it was hoisted up again. While on the bottom, the frame was buoyed because at the depth at which the work was carried on it is practically impossible on an anchored station to keep the ship from swinging excessively. Using a frame set on the bottom has an additional advantage, in that it eliminates the necessity of making a correction for the surge of the ship.

The frame was constructed of 3/4-inch brass pipe with standard fittings. All the other parts were also of brass. There is nothing significant in the dimension of parts or materials used. The bows are fastened at the top by U-bolts to a plate which has a hole in the center to admit the tripping ring. The device for releasing the first messenger was adapted from one constructed by Fridtjof Nansen (Methods for measuring direction and velocity of currents in the sea, Conseil Perm. Internat. Pub. de. circonstance, No. 40, 1906, Pl. II, Fig. 3). The apparatus is operated in the following manner. The line from the surface ends with a ball-bearing swivel to which is shackled a two-part wire-bridle. The longer part is permanently made fast to a U-bolt set in the head-plate, and the shorter part ends in an oval iron ring. This ring is passed through the hole in the center of the head-plate and engages the top hook of the trigger, which is then held in a horizontal position by the weight of the frame, which is now taken by this part

of the bridle. The second messenger is controlled by a push rod which is free to move up and down in guides made of short sections of one-inch pipe, fastened to the under side of one of the legs of the frame. The push rod is just long enough to pass through the topmost guide, which is partly cut away on the under side in order to allow the end of the rod to engage the loop of the wire holding the second messenger. While the frame is being lowered, the push rod is held in place by a wire, which is made fast to the short part of the bridle just above the ring. As this part takes all the weight of the frame during the lowering, the push rod is thus held up and its end kept from slipping past the first guide, thus releasing the second messenger.

When the frame touches the bottom, the short part of the bridle goes slack, and the trigger--no longer held horizontal by the strain on the ring--falls, dropping the first messenger from the lower hook. Releasing the short part of the bridle also slacks the line holding the

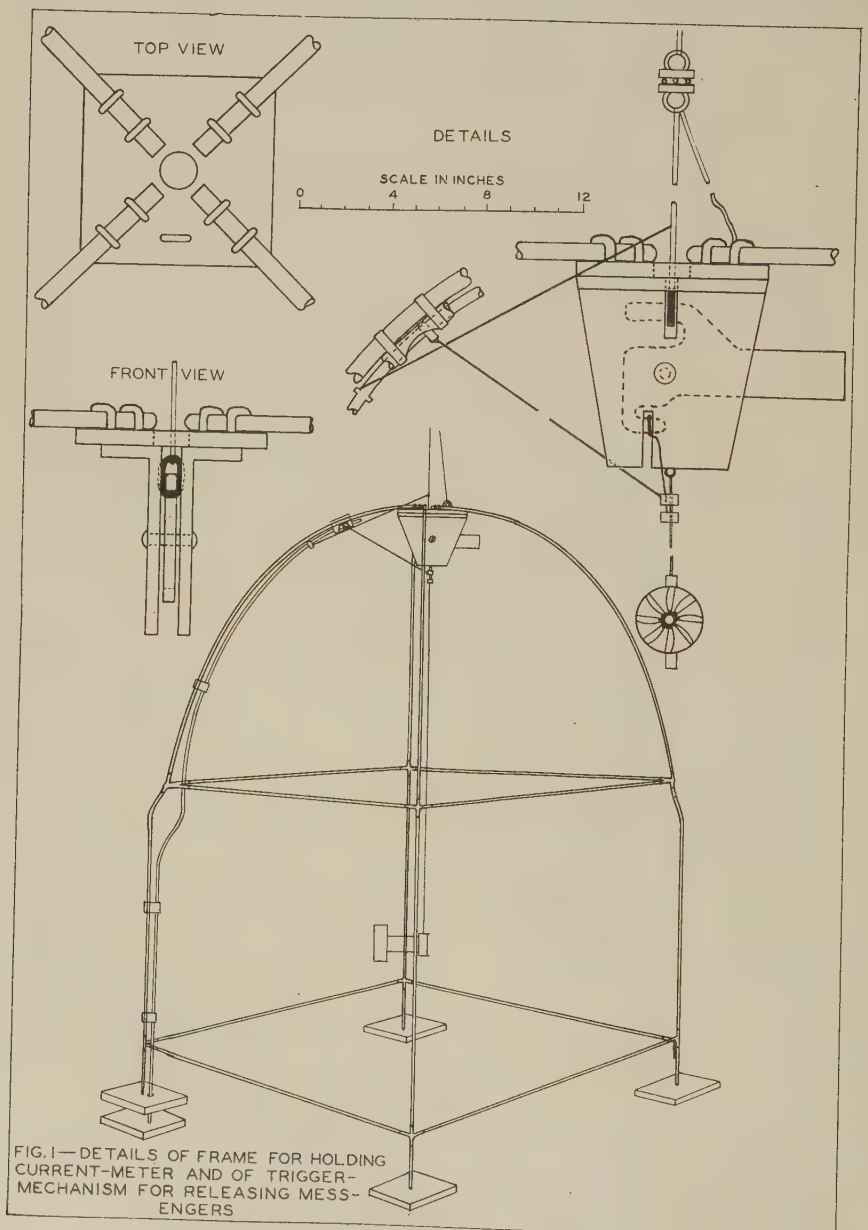

FIG. 1—DETAILS OF FRAME FOR HOLDING CURRENT-METER AND OF TRIGGER-MECHANISM FOR RELEASING MESSENGERS

push rod, which is now kept in place by its foot pressing against the bottom. The frame is hoisted by the long part of the bridle, and as it leaves the bottom the push rod drops down until its end, around which has been passed the loop in the wire holding the second messenger, clears the slot in the under side of the topmost guide--thereby allowing the second messenger to drop. Since it was possible by the feel of the line to tell when the frame touched bottom and when it was completely clear, the time-interval during which the meter was recording could be measured with reasonable accuracy. What slight errors there may have been in timing the arrival and departure were compensated for by allowing the machine to operate for at least 30 minutes.

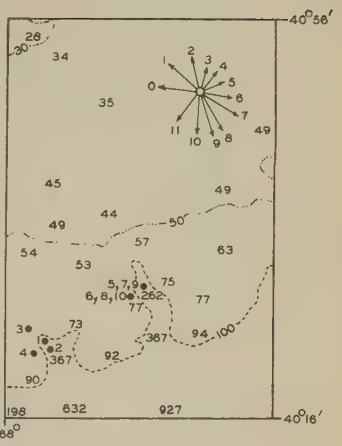

FIG. 2—POSITION OF CURRENT-STATIONS ON GEORGES BANK

When used on Georges Bank the frame was five feet high and about five feet on a side. Later, as in Figure 1, four more feet were added so that readings could be taken at two different levels. The frame had square lead blocks for feet weighing about 10 pounds each. These gave added weight and stability, and at the same time prevented the frame from sinking in on soft bottoms. The center of the propeller was 11 inches off the bottom when the frame was standing on a hard surface. A check on the amount of sinking was made on oozy bottom in Woods Hole Harbor by chalking the sides of the leads. It was found that the feet sank about three-fourths to one inch, and therefore the current in the canyons was measured approximately 10 inches above the bottom. On a bottom of sand or silt, there was no appreciable settling and the current was measured at the full 11 inches.

The 10 stations listed in Table 1 were made in the two canyons cutting the southern margin of Georges Bank between longitude 67° 56' west and longitude 67° 38' west, as well as on the

Table 1--Current-data in the canyons, on the shelf, and at the nearest reference-stations

Station	Date	Direction surface-current at nearest diagram (true)	Direction and velocity in canyons or shelf (true)		Depth	Time at current-station	Interval after high or low water at reference station (Georges Shoal)
			Direction	Velocity			
	1936	°	°	cm/sec	fathoms	h m	h m
1	July 22	115	144 (canyon)	Ebb, 3.12	220	14 55	2 21
2	22	142	214 (shelf)	Ebb, 3.71	73	4 07	4 03
3	24	249	224 (canyon)	Flood, 1.75	230	8 52	1 11
4	24	294	154 to 214° (shelf)	Flood, 12.76	78	10 16	2 35
5	26	278	144 to 164°(canyon)	Flood, 11.08	210	11 10	1 55
6	26	328	? (shelf)	Flood, 5.65	77	12 38	3 23
7	26	33	354 to 4° (canyon)	Ebb, 10.37	260	15 07	5 52
8	26	65	344 to 3° (shelf)	Ebb, 2.31	73	16 24	0 51
9	26	98	154 (canyon)	Ebb, 5.55	260	17 29	1 56
10	26	133	? (shelf)	Ebb, 0.96	77	18 40	3 07

flat surface of the shelf just beyond the canyon-rims. The weather and the requirements of other work prevented more complete observations. The velocities recorded can probably be regarded as somewhat smaller than the average. Weather-conditions were good during the time of observations, and the spring-tides accompanying the new moon on July 18 were beginning to slack off.

The surface tidal currents in this part of Georges Bank are rotary, as is well known, and the diagrams (Fig. 2) on United States Coast and Geodetic Survey pilot-chart No. 70 indicate little decrease in velocity at the turn of the tide. (In Figure 2 the numbers on the current-diagram refer to hours after maximum flood at Pollock Rip Channel, and the arrows give the direction; 1/8 inch equals 1 knot; soundings are in fathoms.) However, some of the readings were taken when the flood or ebb was running full strength, so the maximum possible velocities for those particular days were obtained. The nearest reference-station for tidal predictions is Georges Shoal--some 70 miles to the north. Consequently, the times of high and low water in the canyons will precede it somewhat, and Georges Shoal itself is one hour and 15 minutes ahead of its reference-station, which is Boston. The nearest station for which a diagram of the surface-currents has been made is some 30 miles to the north. While the surface-currents over the canyons are probably not exactly similar, nevertheless one can obtain an approximation of what is taking place. The directions given are all true.

On July 22, at 14^h 55^m, a station was made in the westerly of the two canyons near its head in 220 fathoms. A current of 3.12 cm/sec (about 0.061 knot) was found flowing 144° on the ebb. At the time the station was made, the ebb-tide must have been running about full strength. The surface-currents were running 115°. About one hour later another station was made on the flat surface of the shelf just beyond the edge of this same canyon in 73 fathoms. A current of 3.71 cm/sec was recorded flowing 214°. The surface-currents at this same time were flowing 142°.

Two days later the observations were repeated further down toward the mouth of the canyon. Near the peak of the flood the velocities recorded were 1.75 cm/sec for the canyon in 230 fathoms (0.034 knot) as against 12.76 cm/sec for the shelf (0.25 knot) in 78 fathoms. The current was flowing across the canyon 224° and in approximately the same direction on the shelf, 154° to 214°. At this time the surface-currents were flowing 294°. In this particular canyon the velocities recorded are less than for the nearby shelf.

On July 26 six consecutive stations were made alternately between valley-bottom and shelf in the easternmost of the two canyons. As nearly as possible, the same positions were occupied each time. The depths for the canyon ranged from 210 to 260 fathoms and for the shelf from 73 to 77 fathoms. The flood-tide had been running nearly two hours at Georges Shoal when the first station was made, and for a somewhat longer interval in the canyon as it lies farther offshore. A velocity of 11.08 cm/sec was recorded flowing up the canyon (144° to 164°). The surface-current was already flowing 278°. The next canyon-station was made after high water, but the current was still flowing inwards. A little more than an hour later this lag is still apparent on the shelf as the current there is flowing 344° to 3° and the surface-current 65°. When the next canyon-station was made, a little more than one hour later, the surface-current had only swung to 98°, the current in the valley-bottom was flowing 154°, which is straight out. Scanty and incomplete as the data are, nevertheless two points are brought out. The rotary system of the offshore currents is upset by the topography, which seems to be the controlling factor as far as the canyons are concerned. The flow is now in and out. There is apparently a lag, which is to be expected. Local topography undoubtedly has some effect, but the observations are too scattered to determine its amount.

Let us now consider these currents and their possible effectiveness as agents of erosion. Unlike the first case, the velocities in this canyon are greater than on the nearby shelf. Topographically it is a good deal narrower and longer than the first, and possibly more of a funnelling effect is exerted. The highest velocity recorded on the flood is 11.08 cm/sec (0.216 knot), with 10.37 cm/sec (0.203 knot) the strongest for the ebb. They are below the average as the neap-tides were just beginning on July 26. There is a difference of 40 per cent between the velocities of the spring- and neap-tides, according to the charts of the region issued by the United States Coast and Geodetic Survey. The measurements apply to the surface-currents. If we arbitrarily increase the two highest velocities by this amount, we get 15.51 and 14.52 cm/sec for the spring-tides, which are probably near maximum for the level at which the readings were taken. These values must, of course, be decreased somewhat for the currents actually in contact with the bottom.

As stated above, a velocity of 12.76 cm/sec (0.25 knot) was recorded just before the neap-tides on the flat surface of the shelf where no valley is at present being eroded. On August 8, the day before the neaps, a 13-hour station was made on the shelf 18 miles south of Block Island. At the same level, maximum velocities of 9 cm/sec were found. The soundings over this bottom are regular and give no indication of channelling of any kind.

It would seem, therefore, that the velocities recorded in the canyons are the normal ones which occur on the shelf under present-day tidal conditions. These currents, therefore, are merely flowing in preexisting cuts and are not the cause of them. It does not seem probable that they could be particularly competent agents of erosion when attacking the more indurated material which we know makes up part of the valley-walls. If this be the case in a region of strong tidal currents such as Georges Bank, they would be even less effective farther south where smaller velocities might be expected. Such velocities, however, as are found on Georges Bank would be sufficient to move the finer-grade sizes in an unconsolidated deposit. Hence once the cuts were made, these same currents might be very effective in keeping them open by preventing or checking deposition. On the basis of the above evidence, we are justified in eliminating from further consideration present-day bottom-currents as forces which are capable of forming the east-coast canyons. They may have helped to preserve them, but that is the full extent of the part which they have played. Nor does it seem likely that the type of currents which we have been discussing behaved in the past very differently from the way that they are doing today.

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THE EFFECT OF ITS NITROGEN CONTENT ON THE DECOMPOSITION OF THE POLYSACCHARIDE EXTRACT OF CHONDRUS CRISPUS

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It has been frequently pointed out (Keys, Christensen and Krogh; Johnson; Waksman and Carey, et al.), that the bacterial decomposition of organic matter in stored sea water is limited by the supply of available nitrogen. A rather striking illustration of this arose from an experiment in which the organic material used was the purified polysaccharide extract of the marine alga, *Chondrus crispus,* which provides as well a natural source of nitrogen.

Method

Oxygen consumption was used as the index of decomposition. The customary procedure of storing glass-stoppered bottles (of approximately 200 ml. capacity) under water, at room temperature (20–25° C.), in the dark, was followed. The oxygen remaining was determined by the Winkler titration method, at various intervals. The results given are averages of at least two bottles, more often of three.

Experimental

In a preliminary experiment, the rate of decomposition of the extract was compared with that of the plant itself. The results, given in Table I, show the whole plant to be more readily decomposed than the extract. This fact was attributed to the lower quantity of nitrogen in the latter. For instance, plants containing 1.20 per cent nitrogen, on a dry weight basis, might yield an extract having only 0.30 per cent of nitrogen (Butler, 1936). The method of preparing the extract was described in a previous paper (Butler, 1934).

Table II shows the effect of various amounts of nitrogen, added as nitrate, on the decomposition of the extract.

It is evident from this table that the decomposition was increased in proportion to the amount of nitrogen added, up to a certain point

[1] Contribution No. 144.

only; other factors then apparently become limiting. In seven days the decomposition occasioned with the addition of 0.042 mgm. of nitrate nitrogen was as great as with 0.140 mgm., at least as measured by oxygen consumption. The fact that, with the lower quantity of nitrate, seven days were required to bring about the same amount of decomposition that was accomplished in three days with the larger quantity, suggests a possibility of the nitrogen being utilized more than once. This, however, is not likely, for von Brand, Rakestraw and Renn (1937) have shown that decomposition stops only after an interval varying

TABLE I

Decomposition of Chondrus crispus and its Polysaccharide Extract

Material	Mg. added per bottle	Oxygen consumed (ml. per liter)				
		1 day	2 days	3 days	5 days	6 days
Sea water only	—	0.09	0.24	0.36	—	0.57
Chondrus	3	1.11	1.71	1.89	—	4.32
"	5	—	1.26	—	3.48	—
"	10	1.38	3.60	4.32	—	5.46*
"	20	—	3.18	—	5.88*	—
Extract	25	0.18	0.54	0.81	—	1.47
"	5	—	0.81	—	1.92	—
"	10	0.66	1.17	1.68	—	3.36
"	20	—	1.68	—	5.31	—

* All oxygen consumed.

from 8–20 days. A more probable explanation is that the bacterial population supported by the smaller quantity of nitrogen has a much lower total metabolism than that of the abundant population when nitrogen is more plentiful.

The bacterial numbers given in Table II were furnished by Dr. Margaret Hotchkiss at the Woods Hole Oceanographic Institution, and are simply included here as a matter of record, but will not be discussed.

Having seen the effect on the breakdown of the *Chondrus* extract of adding various quantities of inorganic nitrogen, the effect of different quantities of organic nitrogen became of interest. Since extracts from different collections of *Chondrus* contain varying amounts of nitrogen (Butler, 1936), it was a relatively simple matter to study the effect of this naturally occurring organic nitrogen on the decomposition of the polysaccharide complex. For the purpose, a series of bottles was prepared in which each group contained the extract from a different monthly collection of *Chondrus* plants. As each extract from the plants col-

lected at monthly intervals contained a different quantity of nitrogen, a natural series was provided, in which each member had a different nitrogen content. Furthermore, this nitrogen is in that form in which it most probably occurs under natural conditions, in the plant itself.

Great care was taken to make up each extract in exactly the same concentration, 25 mgm. of extract per liter of sea water. This insured that any individual sample was directly comparable with all the others in the series. Oxygen determinations were made after one day of storage. The results are given in Table III along with the percentage

TABLE II

Effect of Added Nitrate on Decomposition of Chondrus Extract

Extract added (mg. per bottle)	Nitrate nitrogen (mg. per bottle)	Oxygen consumed (ml. per liter)		No. bacteria per ml.
		3 days	7 days	3 days
0	0	0.53	0.74	—
0	0.014	0.55	0.80	90,000
0	0.042	0.55	1.24	—
5	0	1.32	4.07	560,000
5	0.014	3.27	5.02	980,000
5	0.042	4.28	5.28*	—
5	0.140	5.28*	5.28*	3,200,000

* All oxygen consumed.

In this experiment the sea water was enriched by the addition of 1 mg. K_2HPO_4 per liter.

of nitrogen in each sample. It is readily seen that a correlation exists between the two and is most direct where nitrogen is low. This seems, therefore, to furnish definite evidence of the limiting effect of nitrogen on the decomposition of, at least one type of, organic material such as occurs in the sea. It suggests also that the low level of nitrogen during the summer may be partially responsible for the slow rate of decomposition.

While in the present discussion it is assumed that the decomposition is brought about by bacteria, the possibility that the oxygen is consumed by other organisms is not excluded. The water used may, undoubtedly, have contained larger organisms. It was surface water collected in Vineyard Sound and filtered through a No. 25 net of bolting silk. The bacterial considerations cannot be discussed here although evidence was obtained for the bacterial nature of the decomposition. However, the important fact remains that the consumption of oxygen on storing the

polysaccharide extract of *Chondrus* in sea water is correlated with the amount of nitrogen which it contains naturally.

TABLE III

Oxygen Consumption of Various Extracts of Chondrus crispus *

Extract	Nitrogen (per cent dry weight)	Oxygen consumption occasioned in one day by addition of extract (ml. per liter)
January	1.92	0.92
February	2.30	1.05
March	2.40	1.21
April	2.18	1.12
May	1.40	1.09
June	0.82	—
July	0.34	0.23
August	0.37	0.27
September	0.32	0.20
October	0.39	0.24
November	1.28	0.65
November	0.80	0.51
January	2.34	0.80

* The sea water used in this experiment showed an oxygen consumption of 0.55 ml. per liter in one day.

SUMMARY

The decomposition of *Chondrus crispus,* as measured by oxygen consumption, has been shown to be more readily accomplished on storing in sea water than that of its polysaccharide extract. This has been attributed to the higher nitrogen content of the former.

Inorganic nitrogen added to the polysaccharide extract of *Chrondrus* increased its decomposition.

Samples of the extract containing different quantities of nitrogen have been found to decompose in direct proportion to the amount of nitrogen which they contain.

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THE DIURNAL MIGRATION OF DEEP-WATER ANIMALS

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The diurnal vertical migration of planktonic organisms in the sea is a well-known phenomenon (Russell, 1927; Clarke, 1933; 1934).[2] Many more of the actively swimming animals, such as copepods, are found nearer the surface at night than during the day. For example, the level of maximum numbers of adult *Calanus,* in the Gulf of Maine, may be around 40 meters during the night while during the day it may be below 120 meters (Clarke, 1934). It is generally agreed that the most important external factor which regulates these daily movements is light. The greatest depth to which light may have an effect, however, is not known, since almost all studies have been confined to relatively shallow water. Obviously it would depend on the locality and the organisms being investigated, for an animal living at a considerable depth in a region where the water was very transparent might be influenced by the penetrating light, while another organism at the same depth in a region of low transparency would be unaffected. If diurnal migrations occur in deep water they must be considered in any study of vertical distribution. The lowest level at which they occur might be a satisfactory measure of the lower limit of the photic zone. These and other problems of the biology of the deeper water organisms have a direct relation to the possible vertical movements which may occur at levels deeper than any which have been adequately investigated. For these reasons a study was begun of diurnal migrations in deep water during a cruise of " Atlantis " to the Sargasso Sea in 1936.

During the cruise of the " Michael Sars " enough data were obtained from hauls with open nets to indicate that certain of the deep-water fishes and decapod crustaceans were to be found at higher levels during the night than during the day (Murray and Hjort, 1912). The " Michael Sars " data, however, did not indicate how deep such move-

[1] Contribution No. 145.

[2] A rather complete list of references may be found in these papers.

ments might occur, and are conclusive for only a few species of crustaceans and fishes.

The Sargasso Sea was selected for the present investigation since collections with closing nets were being made in this region, and because of the transparency of the water. Helland-Hansen (1931) had found that photographic plates exposed at a depth of 1,000 meters in waters between the Canary Islands and the Sargasso Sea were blackened after an exposure of 80 minutes. Clarke (1936) had calculated from data obtained by Clarke and Oster (1934) that there is sufficient light to enable deep sea fishes to see objects at a depth of 430 meters or deeper in the Sargasso Sea, depending on certain assumptions regarding their

TABLE I

Showing depths, time of day and duration of hauls made with closing nets at "Atlantis" Station 2667.

Haul	Depth	Date	Nets Open	Nets Closed
	meters			
1	400 800	Sept. 6	6:52 a.m.	7:52 a.m.
2	400 800	Sept. 7	4:07 a.m.	5:10 a.m.
3	400 800	Sept. 7	6:57 a.m.	7:57 a.m.
4	400 800	Sept. 7	9:31 a.m.	11:31 a.m.
5	400 800	Sept. 7	1:18 p.m.	3:18 p.m.
6	400 800	Sept. 7	5:10 p.m.	7:10 p.m.
7	400 800	Sept. 7	8:57 p.m.	10:57 p.m.
8	400	Sept. 8	12:39 a.m.	2.39 a.m.
	800	Sept. 8	Net attached improperly, failed to fish.	

visual acuity and spectral sensitivity. Light of an intensity sufficient to affect the general activity of an animal would be found below the level at which objects could be seen.

Since it was desirable to make as many hauls as possible in a twenty-four-hour period only two closing nets were used and they were set to tow at 400- and 800-meter levels. The location of the station (2667) was 35° 40′ N. and 69° 36′ W. The duration of each haul and the time of day may be seen in Table I. One haul was made on September 6 with the nets open at 6:52 A.M. and closed at 7:52 A.M. A rough sea prevented further use of the nets that day but tows were resumed on September 7. The first three hauls were each of one hour duration, but

the absence of salps and other forms which sometimes prevent longer tows, and the relatively small catches made it possible and desirable to increase the time of towing of subsequent hauls to two hours. In order to compare the catches the numbers of organisms taken in hauls 1, 2 and 3 have been doubled.

Since a modification of the closing nets developed and described by Leavitt (1935) were used for these hauls, and since they worked most successfully they will be briefly described and figured. The method of

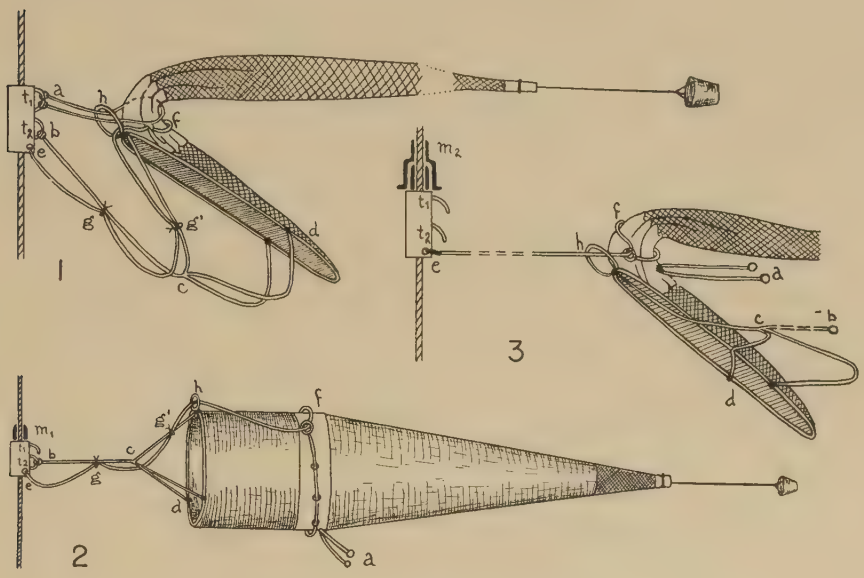

FIG. 1. Net closed, descending.
FIG. 2. Net open, towing.
FIG. 3. Net closed, ascending.

a. Fetter rope.
b. Single towing rope.
c. Three-point towing bridle.
d. Attachment of bridle on two-meter ring.
e. Attachment of pursing rope.
f. Pursing rope around belly-band of net.
g g'. Light string stops.
h. Small iron ring.
m_1. First messenger.
m_2. Second messenger.
t_1. Primary release.
t_2. Secondary release.

opening and closing was the chief feature of this net which differed from the one used by Leavitt. The releasing devices were the same. The changes were made by Mr. Nunnemacher with the advice of Dr. H. B. Bigelow.

The accompanying figures show a net: (1) closed, descending; (2) open, towing; (3) closed, ascending. The net itself has a diameter of 2 meters at the mouth and is laced to a strong galvanized iron ring of 2 meters diameter. The sides of the net are made of stramin (6 threads

per cm.) and are parallel for the first 2 meters and then sewed to a 60 centimeter wide, heavy canvas belly-band to which six 5-centimeter brass rings are fastened at equal distances over the lower half of the band. From the rear edge of the belly-band the net tapers from a 2-meter diameter to one of 25 centimeters over a distance of 7 meters. The end is finished off with another canvas band. Into the end of the net a silk net of corresponding taper is sewed so that it lines the last meter of the stramin and prevents excessive chafing of the catch.

On lowering the net (Fig. 1) a short fetter rope (*a*) fastened at its mid-point to the bottom of the belly-band tightly encircles the folded canvas, passes through the small iron ring (*h*) which is attached to the rim of the net and both ends of the fetter rope are hooked into the primary release. The releasing devices were those previously used by Leavitt (1935) and they proved entirely satisfactory. The loose towing and pursing ropes are "stopped" (loosely tied with cotton string) at points *g* and *g'* to make fouling impossible. After lowering the net to the desired depth, the primary release is opened by the first messenger and the fetter rope easily falls out of the way below the net. The net in opening merely unfolds, the loop of the pursing rope having been previously opened to the diameter of the net at the belly-band and then folded up with it. Figure 2 shows the net being towed by the strong three-point towing bridle and the pursing rope loosely surrounding the belly-band and "stopped" to the towing bridle. A bucket is also shown tied to the end of the net to prevent the tail from fouling in the eddies behind the closed net. After the required time of towing the second messenger releases the towing bridle which falls out of the way. The pursing rope, securely fastened to the cable, now takes the strain, constricts the net at the belly-band and effectively closes the net (Fig. 3).

At each haul an open net was attached 50 meters below the lower closing net. Since the level of maximum numbers of certain of the red prawns and blackfish is near 850 meters in this region of the Sargasso Sea, at least during the day, large catches were always taken by the open net and this material is being used in connection with other studies such as the eyes of deep sea crustaceans (Welsh and Chace, 1937). With the method we used to determine the depth at which a closing net fishes it is impossible to be accurate within about $\pm$ 100 meters at a depth of 800 meters. One can keep the level of the nets relatively constant by so controlling the speed of the ship as to maintain a constant wire angle. But it is not possible to know very accurately the level of fishing because of certain unknown forces which affect the catenary of the wire. We used the calculations made by Leavitt for setting the nets at 400- and 800-meter levels. These were based on the length of towing cable out, the

pull of the nets when open, the weight at the end of the towing cable and the wire angle at the surface.

After sorting the hauls it was evident that some forms had not been taken in sufficient numbers to allow any definite conclusion to be drawn regarding their behavior. Others have not yet been identified. But several of the prawns of the families Acanthephyridæ and Sergestidæ, one of the chætognaths, and the copepods and fishes were present in considerable numbers and the data for these will be presented. The copepods were present in such very large numbers in some hauls at the 400-meter level that their numbers were estimated in those hauls and no attempt was made to separate and identify the several species. Fishes at 800 meters were also present in large numbers and counts were made of these in each haul but again they were not separated into genera or species. In spite of dealing with mixed populations of copepods and fishes, the data readily convince one that the more abundant species behave in a consistent manner and that their movements are obviously related to day and night. A remarkable correlation in the numbers of copepods and fishes in the separate hauls at the 400-meter level will be discussed later.

In the graphs the total number of animals of a group such as copepods, or of a species, where separations into species were made, taken in any haul is shown by a vertical bar. Haul 1 made on September 6 from 6:52 A.M. to 7:52 A.M. serves as a check on the consistency of catches from day to day as another haul was made on September 7 from 6:57 A.M. to 7:57 A.M. The lined bars represent the September 6 catches. When no representatives of a given species were present the word "none" appears in place of a bar. The net at the 800-meter level at the last haul made on September 8 from 12:39 A.M. to 2:39 A.M. failed to work as it was improperly attached; hence no data are available for this time and depth. The time of sunrise was 5:37 A.M., of sunset 6:19 P.M. at the position of this station on September 6. A heavy line at the bottom of each graph indicates the hours between sunset and sunrise, but it should be remembered that at any considerable depth the period of relative darkness would be longer than at the surface (Clarke, 1934). It should also be noted that haul number 6 began before sunset and continued some time afterward. Further remarks concerning a particular species or group of animals may best be made under separate headings.

Acanthephyridæ (Fig. 4)

The complete absence of any of the large red prawns from hauls made during the day at 400 meters was the first reassuring evidence that our results would add more convincing weight to the conclusions reached

by Murray and Hjort (1912). *Systellaspis debilis* and *Acanthephyra purpurea* had been taken previously in this region of the Sargasso Sea (Welsh and Chace, 1937) but in these earlier collections with closing

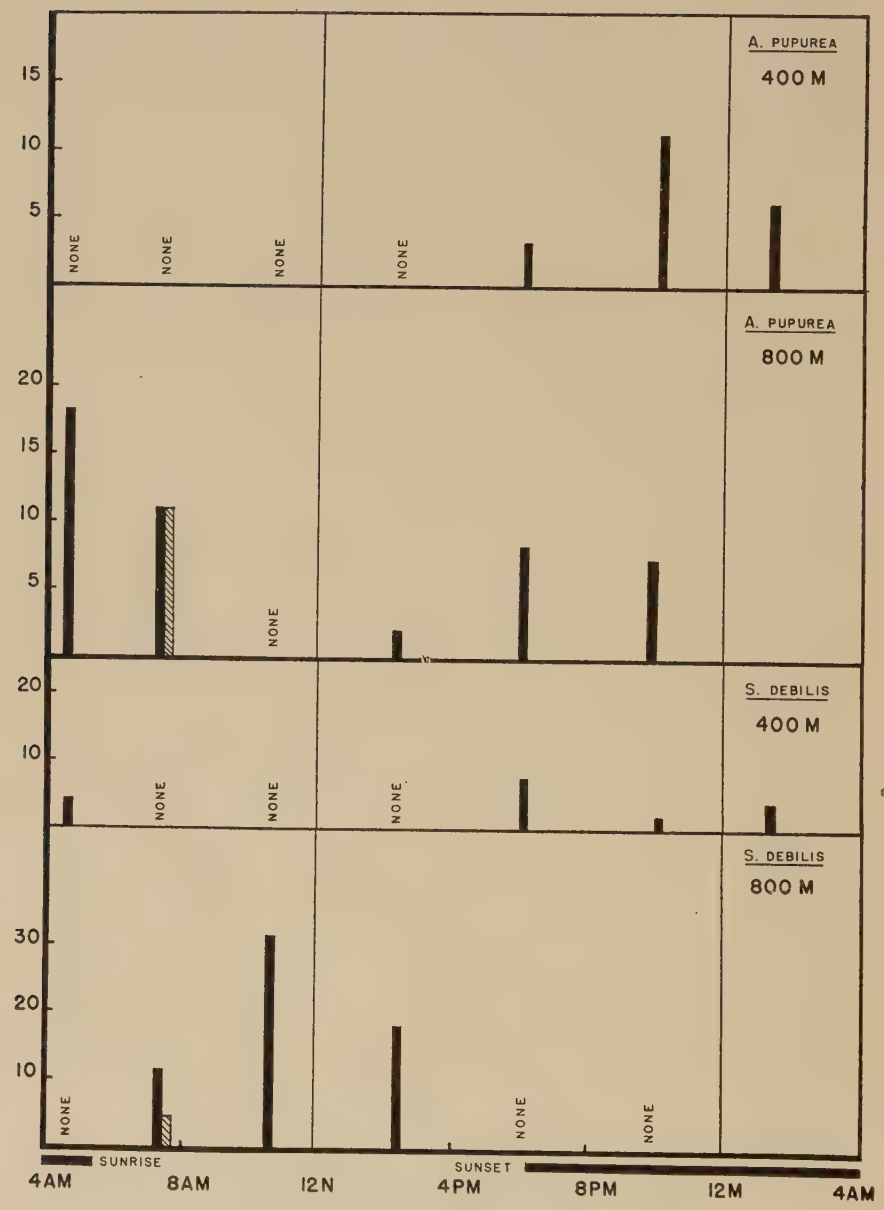

Fig. 4.

nets little attention had been paid to the time of day when the hauls were being made. At 800 meters the largest catch of *A. purpurea* was made in the early morning before sunrise, none were taken in the haul made nearest midday. On the other hand, *S. debilis* was taken at 800 meters only during daylight hours. Since it is known that *S. debilis* occurs at a somewhat higher level than *A. purpurea* a comparison of the catches of these two forms at the two levels strongly suggests that during the day the majority of *S. debilis* descend to a depth around 800 meters and the majority of *A. purpurea* to a somewhat greater depth.

Both *A. purpurea* and *S. debilis* have well-developed eyes. In contrast another acanthephyrid, *Hymenodora glacialis,* with degenerate eyes, has never been taken with closing nets from " Atlantis " at levels higher than 1,000 meters. It is an example of a form which has become adapted to a region below that at which penetrating sunlight has an effect on behavior and the development of the eyes. The upper limit of its distribution suggests that 1,000 meters is approximately the depth to which a biologically significant amount of sunlight can penetrate in water as transparent as that of the Sargasso Sea.

Sergestidæ (Fig. 5)

Of the sixteen species of *Sergestes* recorded from the North Atlantic, thirteen were taken at Station 2667. Of these thirteen, three species were taken in numbers large enough for statistical study. *Sergestes sargassi* appeared only in hauls at the 400-meter level and then only in those made during daylight hours. It was most numerous in the hauls made soon after sunrise. As this is known to be a comparatively shallow water species, it appears that it moves toward the surface during the night and returns to a depth around 400 meters during the day.

S. atlanticus was taken at the 400-meter level in two night hauls and in the haul which extended from about an hour before sunset until an hour after. None were taken at this level during the day. For some reason no sergestids of any species were taken in haul 7 at the 400-meter level in the late evening. At 800 meters *S. atlanticus* appeared in considerable numbers in the hauls made during the day, but except for one specimen which was taken in haul 2, none appeared in the other night hauls. Evidently this species migrates to deeper water during the day than does *S. sargassi.* It should be added that *S. atlanticus* has been taken in surface hauls made during the night.

The catches of *S. corniculum* at 400 meters were very much like those of *S. atlanticus* as regards relative numbers and times of appearance. At 800 meters, however, *S. corniculum* was found in relatively large numbers in all hauls during both day and night. It would appear

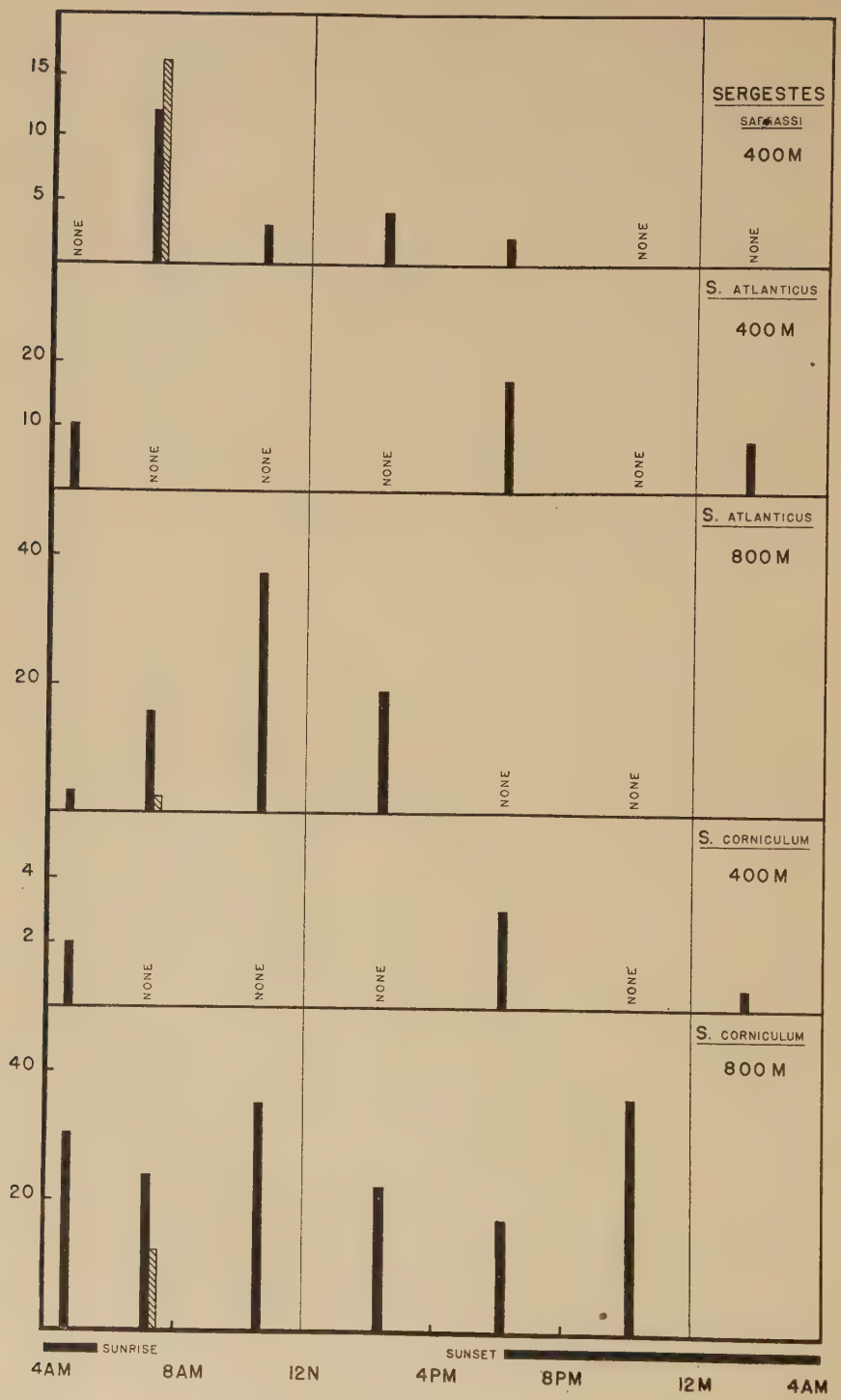
15
10
5
NONE
NONE
NONE
NONE
SERGESTES
SARGASSI
400M
20
10
NONE
NONE
NONE
NONE
S. ATLANTICUS
400 M
40
20
NONE
NONE
S. ATLANTICUS
800 M
4
2
NONE
NONE
NONE
NONE
S. CORNICULUM
400 M
40
20
S. CORNICULUM
800 M
SUNRISE
SUNSET
4AM
8AM
12N
4PM
8PM
12M
4AM

FIG. 5.

that it was a form that migrated less extensively than some of the other species of *Sergestes.* That there are sergestids which are found below a level to which a sufficient amount of light penetrates to cause any diurnal vertical movements is known from our records on *S. mollis.* This species has been taken with closing nets only at depths of 1,600 meters and greater. Thus we see in this series of sergestids that the level of maximum numbers depends on the species and the time of day or night; also that the average depth at which a given species may be found depends on the extent of daily migration, if it occurs at all.

Copepods and Fishes (Fig. 6)

Because of the number and variety of fishes they have not been separated into species and neither have the copepods. These two distinctly different types of animals show, at the 400-meter level, a very similar type of distribution at different times of day and night, and this correlation may be seen if the graphs in Fig. 6 are examined. The largest catches were taken at the 400-meter level in the haul made just before sunrise and the one which extended from about an hour before until an hour after sunset. Most of the other catches when compared with these were small. It is probable that the large catches were taken as the migrating copepods and fishes passed the 400-meter level on their ascent and descent. The very large catches before sunrise must mean that these animals anticipate the return of dawn and start downward before there is any increase in light intensity. When the numbers of fishes taken at 400 and 800 meters are compared it is first obvious that many more were taken at the deeper level, and then that many more were taken during the day than during the night. It is probable that this depth is not very far from the daytime level of maximum numbers of deep-water fishes of this region. The striking correlation in numbers of copepods and fishes at the 400-meter level suggests that the fishes move with the copepods and thereby stay near their chief food supply.

Sagitta hexaptera (Fig. 7)

One large, easily recognized chætognath, *Sagitta hexaptera,*[3] was separated and counted and will serve as another example of a form which was taken only at 400 meters. On examination of the graph of the distribution of this form it is seen that the largest catches were made near midday, the smallest in the late afternoon and early evening. It would seem that the level of maximum numbers of this species was in

[3] Identified by Miss Alice Beale.

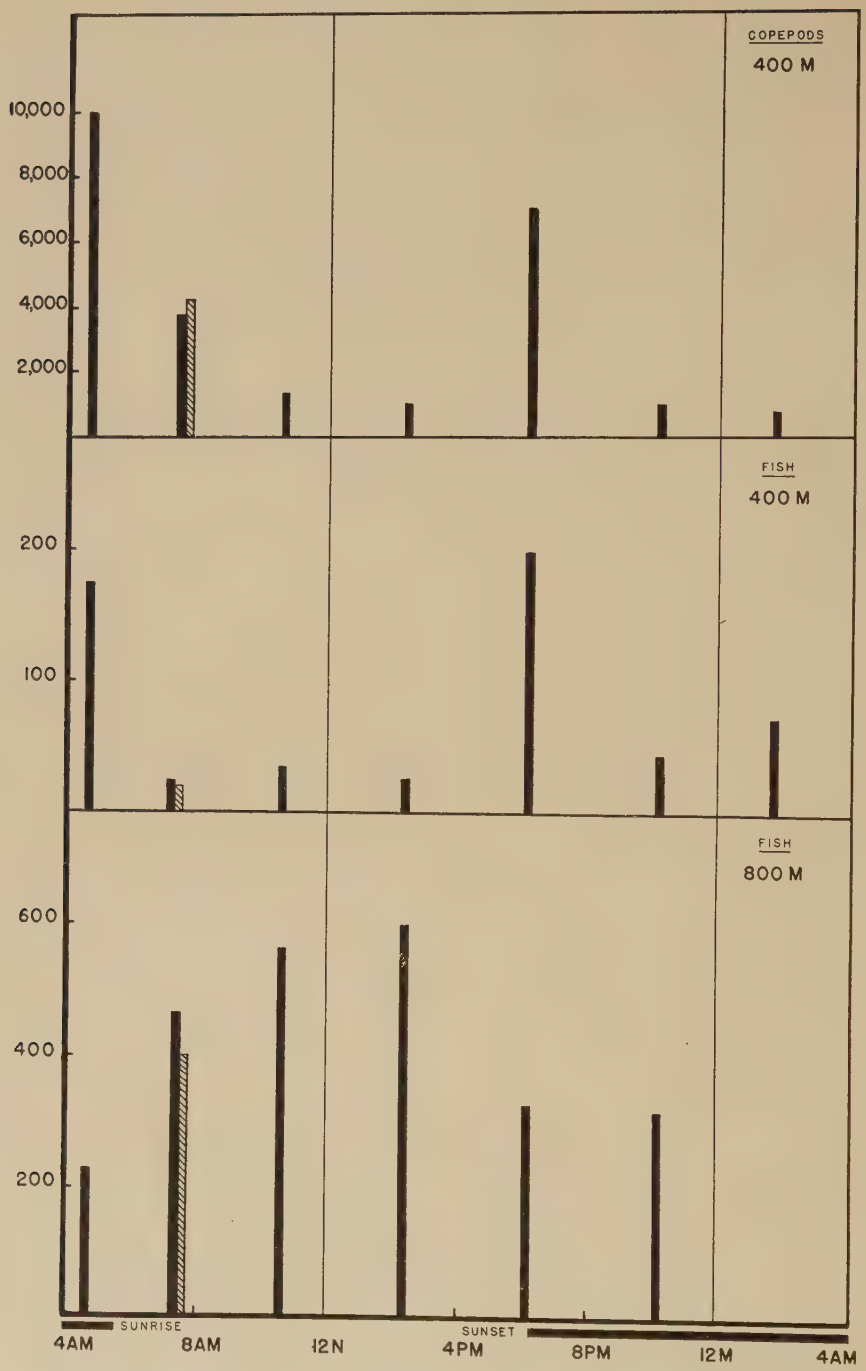
COPEPODS
400 M
10,000
8,000
6,000
4,000
2,000
FISH
400 M
200
100
FISH
800 M
600
400
200
SUNRISE
SUNSET
4AM
8AM
12N
4PM
8PM
12M
4AM

Fig. 6.

water shallower than 400 meters during the night and that they descended to near this level during the day.

Day to night differences in the numbers of certain species and groups of organisms, at depths of 400 and 800 meters, indicate not only that the animals of the deeper water of the Sargasso Sea migrate as do those of the shallow water, but that for certain species these daily migrations may be over a considerable distance. Light is probably the only day to night variable at a depth of 800 meters, or approximately one half mile; hence differences in light intensity must be largely responsible for these movements. There is, however, some indication that deep-water animals anticipate sunrise as Clarke (1934) found certain shallow water forms such as *Metridia* to do. This suggests that a physiological rhythm may

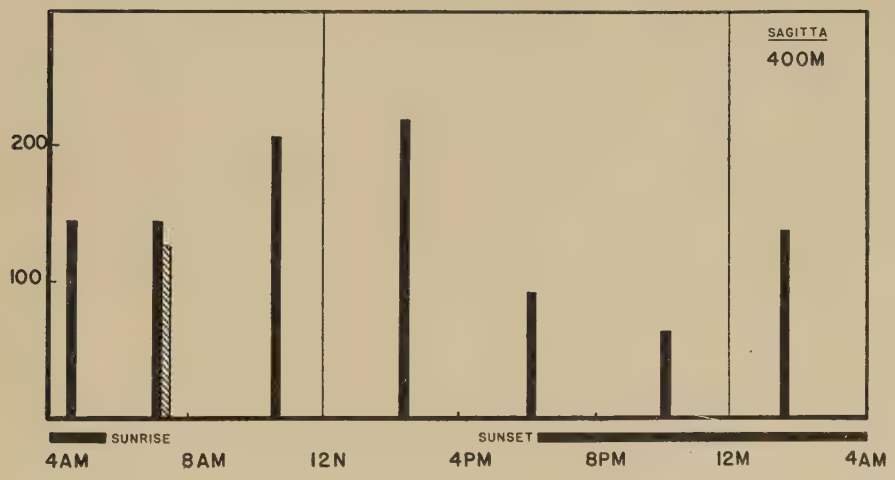

Fig. 7.

in part be responsible for their behavior. Diurnal rhythms are known to persist for considerable lengths of time in the absence of regularly recurring changes in light intensity (Welsh, 1936). An internal cycle resulting in periodic changes in activity would account for the downward movement which begins before there is an increase in light intensity.

Many questions have arisen which can be answered only by further investigations. It will be of interest to determine the greatest depth at which daily migrations occur and to correlate these movements with measurements of light intensity. It will be necessary to make collections at many more levels before final conclusions can be drawn regarding the behavior of the organisms discussed in this paper, and of the many which have been omitted from this discussion. Possible differences in

the behavior of animals with and without light organs should be investigated. The lower limit of the penetration of light of an intensity significant in determining the vertical distribution of animals should be correlated with the rather marked changes in temperature, salinity, oxygen and phosphates which occur at depths near 1,000 meters in certain parts of the Sargasso Sea. A combination of factors is doubtless responsible for keeping the majority of the macroplankton above 1,000 meters in this region, but it would be of interest to know which one, if any, is most important.

The collection and analysis of data of this kind is inevitably slow, but the vertical movement of organisms in the sea is of practical as well as of theoretical importance since the nightly aggregation of organisms near the surface increases greatly the potential food supply of surface fishes. Further work in the Sargasso Sea is planned and it should be possible to obtain a much more complete idea of the biology of deep-water organisms than we now possess.

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BEHAVIOR OF SUSPENSION CURRENTS AND MUD SLIDES ON THE CONTINENTAL SLOPE.

H. C. STETSON AND J. FRED SMITH.

(Contribution No. 146 of the Woods Hole Oceanographic Institution.)

ABSTRACT.

Density currents due to sediment in suspension, which have recently been discussed by Daly in considering the origin of submarine canyons, have another important implication. Once the sediment is in suspension the current, in a stable ocean, will flow down the continental slope until it reaches a layer with a density greater than its own. It will then spread out horizontally over the top of the heavier layer. Therefore, regardless of the ability of currents of this type to erode, they may be important agents for the distribution of sediment over the continental slope and nearby ocean floor.

Calculations have been made as to the amount of sediment which must be placed in suspension to enable the resulting current to flow beneath the water which lies against the continent, and so reach the bottom of the slope. The density of the ocean water increases with depth.

Seepage as a possible factor in submarine slumping is also discussed, together with the effects of repeated slumps on the configuration of submarine canyons.

INTRODUCTION.

The theory of density currents recently proposed by Daly to account for the origin of submarine canyons has an important implication which the writers feel has not been sufficiently stressed. Regardless of whether or not these currents possess sufficient erosive power to cut the great gorges, by their very nature they must be competent agents for the distribution and deposition of terrigenous sediments over the continental slopes and neighboring ocean bottoms. Their importance in this capacity has been largely dwarfed by the interest in the controversy over the origin of the canyons themselves. Yet, the mechanism proposed by Daly will not only operate during the special conditions of the Pleistocene, as he postulated for the case of canyon formation, but during and after every big storm, both now and in times past. Once sediment is put in suspension in some portion of a body of water, that portion,

other things being equal, becomes relatively denser and tends to seek the lowest possible level, displacing the lighter water. The movement may be slow, but the muddy water must move. It is proposed that density currents of this type be called "suspension currents."

Seepage as a possible factor in submarine slumping has received scant attention. Although it has no direct connection with the action of the currents under discussion, both have some bearing on the problem of the origin of the canyons. It is pertinent, therefore, to the general subject in hand.

SUSPENSION CURRENTS IN THE SEA.

Briefly, Daly's reasoning is as follows. During the times of lowered sea level of the Pleistocene, large areas of unconsolidated, fine-grained deposits on the continental shelf and slope which formerly had lain below wave base, were within reach of wave action. Large quantities of sediment were thrown into suspension by the storms of that period. This heavier, denser water would first seek the depressions of the shelf, such as might have been due to the initial irregularities. It would concentrate and run down them, and eventually flow over the continental margin and down the slope with greatly accelerated motion.[1] It might conceivably develop sufficient velocity to erode grooves and later, trenches. In a recent paper Kuenen strongly supports the idea that these currents may be competent agents of erosion, basing his arguments on tank experiments.[2] Whether or not these currents are capable of cutting the canyons is beyond the scope of this paper. We are only concerned with the actual operation of this type of current regardless of its velocity.

Let us now consider what will happen to suspension currents travelling down the continental slope. The generalized curve in Fig. 1 shows the normal changes in density, corrected for temperature, over the continental slope from Sable Island to Cape Hatteras. The effect of compression was not taken into account, as at any given depth the suspension currents are subject to nearly the same increase in density as the surround-

[1] Daly, R. A.: Origin of Submarine Canyons, This Journal, Vol. 31, pp. 400-420, 1936.

[2] Kuenen, Ph. H.: Experiments in connection with Daly's Hypothesis on the Formation of Submarine Canyons. Leidsche Geol. Mededeelingen, Deel. VIII, Aflevering 2, Blz. 327-351, 1937.

ing water. The water of the deep ocean is stable and little mixing takes place between the different layers. The lighter water covering the shelf in summer is due to higher tempera-

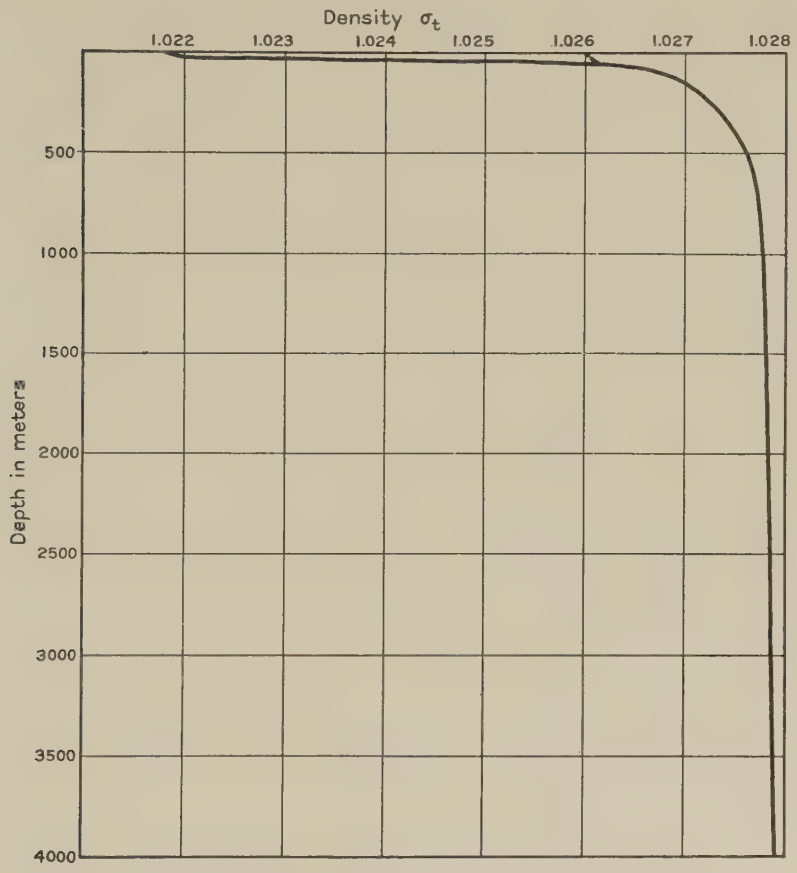

Fig. 1. Normal changes in density with depth (not including the effects of compression) for the waters over the continental shelf and slope from Sable Island to Cape Hatteras. In winter the curve terminates at 1.026 but in summer it continues to 1.022.

tures, and at this season it is well stratified. In winter the density all over the shelf is raised to 1.026 by cooling, and the water is uniformly mixed from top to bottom by the strong gales which are now common. Below 50-100 meters there is

no seasonal variation. Winter is therefore the most favorable time for muddy water to sink to any considerable depth, as the shelf water is heavier to start with, and needs the addition of relatively smaller amounts of sediment. For the data from which this curve is constructed the writers are indebted to C. O. Iselin of the Woods Hole Oceanographic Institution. It is based on observations obtained by the research ship "Atlantis" of the same Institution.

Daly's mechanism is set in motion as the result of the energy which a storm is able to expend on the bottom through wave-generated currents. Once the particles of sediment are in suspension, and the stream has started down the slope and left the zone of wave action, its initial density is affected by a variety of factors. Will extensive deposition now take place or will the stream start cutting, thereby adding to its load? The velocity is determined by the density of the original suspension and by the angle of the slope down which the stream flows. The textures of the bottom sediments will also have their effect. Variations in the angle of bottom slope, diffusion into the surrounding water, turbulence, and frictional resistance likewise affect velocity. In addition, as the stream flows down the slope, the surrounding water at its successive levels becomes increasingly denser. A quantitative evaluation of the forces involved is impossible at present, but whatever may be the sum-total effect on the actual velocities, the current will continue to move downwards, even if it is reduced to a very slow drift, until it reaches a layer of greater density than its own. It should then spread out horizontally along the top of the denser layer, continuously losing sediment by settling, and, having definitely left the bottom, it has no further chance of picking up more. Its velocity is now dependent on the momentum it has been able to acquire. It should gradually lose speed until it finally merges with currents of other types. Even though a current never reaches the great depths, it can still be an effective distributor of sediment over the continental slopes and the nearby ocean floors.

The action of currents of this type explains why the depressions in an irregularly floored basin, like the Gulf of Maine, are filled with fine-grained deposits. Any sediment-laden water produced by wave action must immediately seek the lowest possible level, and if the depressions are free from current scour the sediments, once deposited, will remain there.

TANK EXPERIMENTS.

In a tank measuring 3 by 3.5 feet a "continental shelf" was constructed nearly flat at the top and with an outer "slope" of about 25°. The differences in the densities between the layers of water used in the model are of necessity far greater than would ever occur in the ocean. There is, therefore, nothing significant in the figures by themselves. Neither the scale of Nature nor the time element can be reproduced. Nevertheless, the tests serve to illustrate the principles involved, although the proportions are different from those found under natural conditions. All densities in the tests were determined with a set of Knudsen hydrometers, and the figures here and in Fig. 1 have been reduced to the same basis (*i.e.*, the specific gravity of sea water at 0° C. referred to distilled water at 4° C.) by the use of his tables, as well as corrected for temperature. Several trials were made but the two cited below are sufficient to serve as illustrations.[3]

Sea water was poured into the tank to a depth of six inches and over it was flowed an equal layer of tap water. A small amount of mixing occurred at the junction between the two layers when the fresh water was flowing in, but once the slight turbulence had subsided, they remained stable. Water samples were taken three inches below the surface and three inches above the bottom. The fresh layer which originally had a density slightly greater than distilled water showed a slight increase, but at the level sampled the salt layer remained unchanged. In the two cases considered here the densities of the top layers were 1.00651 and 1.00286 respectively, and that of the bottom, 1.01968 and 1.02121. Tap water carrying a suspension of mud was introduced on the top of the "shelf." The corrected hydrometer readings were 1.01735 and 1.01702.[4] The sheet of denser water spread slowly towards the "break in slope" and once over that point, started to run downwards beneath the lighter water with greatly accelerated motion. When a layer with a density of 1.00779 and 1.00457 in each of the respective cases was reached, the stream left the slope and started to spread out horizontally in the tank. A sample from the muddy stream itself, which by this time was somewhat saline, gave the same values. The decrease in density

[3] Knudsen, Martin: Hydrographical Tables, Copenhagen, 1901.

[4] These figures are not referred to the same basis as the others, because Knudsen's tables only apply to saline solutions. However, the order of magnitude is not affected.

from that of the original suspension was in the main due to deposition, and to a lesser degree to diffusion into the surrounding water. The small irregularities and depressions on the "shelf" and "slope" were full of mud, but the ridges in general were bare. Deposition continued after the stream had left the bottom. Due to the coagulating action of the electrolytes in the sea water, flocks of the fine-grained material were dropped from the bottom of the sheet through the denser water below.

ESTIMATED QUANTITIES OF SUSPENDED SEDIMENT NECESSARY TO PRODUCE CURRENT MOVEMENT.

Some quantitative data would be of service in a consideration of the densities of the ocean relative to the amounts of material which must be added to the water near the beach to raise its density sufficiently to cause it to flow down the shelf and to the bottom of the continental slope. These data may be obtained by means of the following equation derived by Casagrande in working out his technique for the mechanical analysis of fine-grained sediments by means of an hydrometer.[5]

$$\sigma = \delta + \frac{W(S-\delta)}{VS}$$

where σ is the resulting density, δ is the specific gravity of the water to which the material is to be added, W is the weight of the added material, S is the specific gravity of the added material, and V is the total volume. This equation is based on the assumptions (1) that "Stokes' Law is valid," (2) that "the suspension is uniform at the start of the test," and (3) that "the area of sedimentation cylinder is large compared with the cross-section of the hydrometer tube."

As a check on the equation, density measurements by the hydrometer were made on a suspension composed of a weighed quantity of bentonite mixed with distilled water. By means of the equation the values for the same figures were obtained. Knudsen hydrometers may be read to the fifth decimal place. Table 1 gives the results obtained directly and also those determined from the equation. The validity of the equation is shown by the fact that the two sets of values agree rather closely.

By the same equation may be determined the amount of

[5] Casagrande, A.: Die Aräometer Methode zur Bestimmung der Kornverteilung von Boden. Berlin, Julius Springer, 1934.

TABLE I.

Test No.	Hydrometer Measurements		Determinations by the equation	
	Density (gms. per cc.)	Weight (gms. per 1000 cc.)	Density (gms. per cc.)	Weight (gms. per 1000 cc.)
1	1.00573	8.94	1.00575	8.89
2	1.00634	9.97	1.00641	9.86
3	1.01263	19.61	1.01260	19.64

A comparison of the density measurements by the hydrometer method, with the determinations obtained by the equation.

material which must be suspended in the near-shore water to increase its density sufficiently to allow it to flow down the slope into the denser layers of the ocean. In this case the latter two assumptions upon which the equation is based are even more valid than in the case of the hydrometer measurements; a unit volume (say 1000 cubic centimeters) of ocean water will probably retain the material in a fairly uniform suspension, and the size of the sedimentation cylinder need not be considered. The problem as solved here represents the ideal conditions. The assumption is made that the density of the near-shore water, produced by the addition of suspended material, remains constant throughout its descent of the slope; that is, there is no loss of material by deposition, no gain of material which might be stirred up along the bottom by the suspension current, and no change in salinity. First the generalized densities during summer for the water over the continental slope are taken (1.022 grams per cc. near the beach, 1.023 grams per cc. at about 30 meters depth, etc. Fig. 1). The specific gravity of the added material is taken as 2.6, as this value has been found to be a good average figure for the sediments from the east-coast shelf of North America. As an example, the following problem shows the determination of the amount of material with a specific gravity of 2.6 which must be added to 1000 cc. of the near-shore water (density 1.022 grams per cc.) to cause it to flow to a depth of about 30 meters, where the density of the water is 1.023 grams per cc.:

$$\sigma = \delta + \frac{W(S-\delta)}{VS}$$

$$1.023 = 1.022\,\frac{W(2.6-1.022)}{1000 \times 2.6}$$

$$W = 1.65 \text{ grams.}$$

To raise the density of the water near the shore sufficiently for it to flow to a depth of 40 meters (density, 1.024 grams per cc.) 3.29 grams would have to be added to 1000 cc. In order that the currents may reach the floor of the ocean, where the density is 1.028 grams per cc., 9.88 grams per liter of sediment must be held in suspension. In winter, however, as the water at all depths over the shelf has increased to a density of 1.026 grams per cc., only 3.29 grams per liter need be carried for the suspension current to flow to a depth of 4000 meters. (For the other values see Table 2.) These figures show that about 1.65 grams per liter must be added successively to raise the density 0.001 grams per cc. This amount, however, cannot be taken as a standard value, because the number of grams necessary to change the density 0.001 varies with the specific gravity of the material added.

TABLE II.

Densities in North Atlantic Ocean at various depths		Volume in cc. per liter				
		1.022 Min. Summer Density		1.026 Winter Density uniform to 50 m.		1.0 Distilled water
Depth (meters)	Density (gms. per cc.)	Grams	Vol.	Grams	Vol.	Grams
30	1.023	1.65	0.63	...	...	37.40
40	1.024	3.29	1.27	...	...	39.02
45	1.025	4.94	1.90	...	...	40.65
50	1.026	6.59	2.53	...	...	42.28
150	1.027	8.24	3.17	1.65	0.63	43.90
4000	1.028	9.88	3.80	3.29	1.27	45.53

Amount of sediment (specific gravity 2.6) which must be suspended in one liter of shelf water, and in distilled water, to raise the densities sufficiently to exceed the densities found in the North Atlantic Ocean in summer and winter.

In the above table the determinations were made only to a depth of 4000 meters, since below that depth the density changes in the North Atlantic Ocean are negligible. Column five was inserted to show the much greater amount of added material necessary to raise the density of distilled water to meet the required values of the ocean densities. It is evident that a river entering the sea would have to carry a very heavy load in order to create a suspension current.

The values in Table 2 cannot be compared with the actual densities produced by the stirring up of mud in the North Atlantic, because no measurements of such suspensions have been made on the continental shelf and slope. However, they

do not seem to represent unreasonable amounts of suspended material. Density measurements in many rivers show that the suspensions there can be much more concentrated than are those listed in the table. Consequently, it is probable that as the bottom is constantly stirred by storms, suspension currents gradually carry sediment off shore, and that at times they flow to considerable depths in the ocean. During the Pleistocene, under the conditions postulated by Daly, they would, of course, be much more vigorous than at present.

SLUMPING.

Landsliding has been suggested many times as a mode of origin for submarine valleys. This theory, however, has been strongly criticised by Shepard because the dendritic form of the canyons, as revealed by recent surveys, does not conform to features produced by similar processes on land. Slides might be called on for removing unconsolidated sediment from a partially filled canyon, but they could not produce the original shape.[6]

In the course of the tank experiments certain things were observed which make it seem worth while, in spite of the apparent difficulties, to bring up once more the part which slumping may have played in canyon formation. The authors are well aware that this cannot be accepted as a general explanation, but when a situation arises wherein all the theories advanced for a major problem such as this encounter serious difficulties at some stage, no possible contributing factor can be ignored.

Daly has discussed the matter to some extent. He considers the possibility that the canyons may be the joint product of suspension currents and the localized sliding of sediment that was much diluted with sea water. The current's drag on the bottom might be sufficient to "trigger off the potential energy of sediments that stood high above the floor of the deep ocean and were ready to slide if urged by a comparatively small force." The combination would place more mud in suspension and so "increase the drag as well as the cutting power of the original current."[7]

The "continental shelf" used in the density work was constructed of sand with a surface layer of about one half an

[6] Shepard, F. P.: Canyons off the New England Coast, This Journal, Vol. 27, pp. 24-36, 1934.
[7] Daly, R. A.: Op. cit., p. 412.

inch of clay that had settled from the overlying water. When the water was being siphoned from the tank and the top of the "shelf" just emerging, slumping occurred towards the bottom of the "slope" in the clay layer, parts of which slid off, carrying some of the underlying sand with it. As the water level fell, the flocculent top of the clay layer slid down with it,

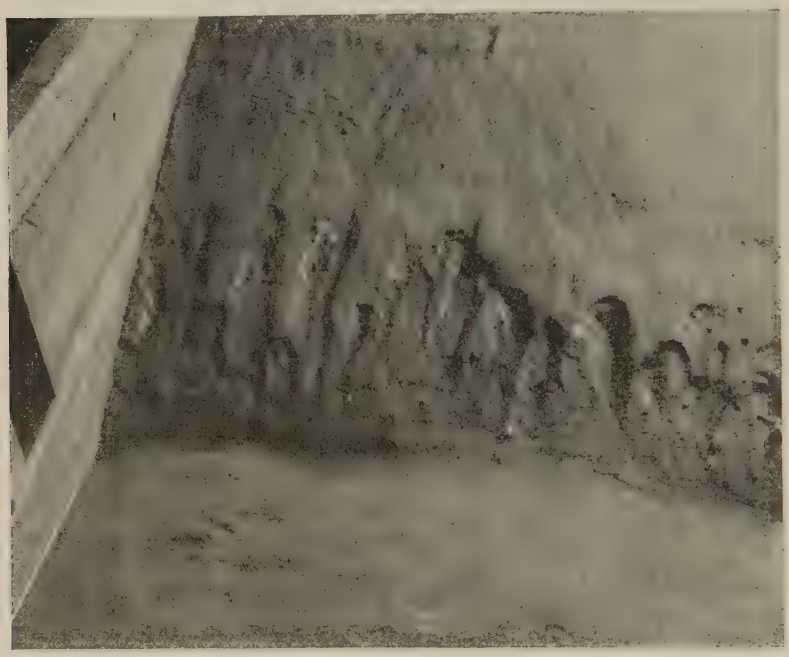

Fig. 2. "Canyons" produced under water by slumping initiated by seepage.

eventually forming streams of mud which flowed down the slope under their own momentum. These ran over the small scarps produced by the initial slumping and eroded the sand below. The trials were repeated many times, and between each run the clay in the bottom of the tank was stirred up and allowed to resettle, forming a new layer over the surface of the "shelf." Each time the layer slumped at exactly the place that the first breaks had occurred, and this process, combined with small slides coming down from above, further scoured out the bottom of the small "landslide valleys." (Fig. 2.) They do not have, it is true, the shape of most of the submarine

canyons; rather, the heads are lunate. However, it is not the shape which is the significant thing, but the effects which sliding will produce—whatever may be the cause.

In this case, the head produced when a small portion of the "shelf" emerged from the water caused seepage at lower levels, thereby stripping off the outer layer in some zone of weakness. The "shelf" of sand was pervious and the clay covering impervious. When a glass tube connected with an aspirator was inserted into the "shelf," and outward seepage through the sand checked, slumping ceased. The situation is a familiar one to engineers, and in the construction of earth dams the question of upstream slumping must be carefully considered.

In the model the relatively large head, the rapid lowering of "sea level," and the very poor shearing resistance of the thin clay layer, provide a ratio of forces which probably could not be duplicated under natural conditions. It is unlikely, therefore, that in the ocean slumping could be produced by this cause alone. The head produced by an emerged continental shelf would not be sufficient to overcome the shearing resistance of the material on the slope. However, the structure of the Coastal Plain with its nearly horizontal, pervious layers overlain at the continental margin by newly deposited silts and clays makes seepage a factor to be considered. Even if not sufficient by itself to initiate slumping, in combination with other forces, it might be enough to tip the balance. Could sea-level be lowered as fast as water falls in a reservoir the whole face of the continental slope would undoubtedly slide into the ocean basin.

Another possible result of slumping might be mentioned, which would be of advantage to the proponents of cutting by submarine currents. The hard layers found outcropping in the canyon walls, admittedly a difficulty to theories of erosion under water, can be removed without cutting. As Kuenen points out, if they were undermined by slumping, they would fall of their own weight.[8] In fact during dredging operations in the east coast canyons the senior author has several times found talus blocks of the harder strata lying at the foot of the cliffs. This may be a small scale illustration of the above process.[9, 10]

[8] Kuenen, Ph. H.: Op. cit., p. 349.

[9] Stetson, H. C.: Geology and Paleontology of the Georges Bank Canyons, Pt. 1. Bull. Geol. Soc. Amer., Vol. 47, pp. 339-366, 1936.

[10] Dredge samples from the Submarine Canyons between the Hudson and the Chesapeake. Trans. Amer. Geophysical Union, 17th Ann. Meeting 1936. Oceanography, pp. 223-225, 1936.

Submarine landslides on a major scale are known to occur, as for instance the one which broke the Western Union Telegraph Company's cables off the Grand Banks of Newfoundland following the earthquake of November, 1929. Small ones and minor slumps due to a variety of causes probably occur frequently, and pass unnoticed. Under natural conditions slumping, long continued, might have considerable erosive effect in valleys which had been cut in strata similar to that of the emerged portion of the Coastal Plain.

CONCLUSIONS.

Whether or not the suspension currents proposed by Daly are sufficiently powerful to erode submarine canyons, they must be important agents for the transportation and distribution of marine sediments. Great variations in the amount of mud thrown into suspension must occur with different storms, but, even if the load is small and the current is reduced to a drift, it will continue to move downwards in a stratified ocean until it reaches water of greater density than its own. It will then move out over the top of this heavier layer, but its effectiveness as a distributing agent is not diminished, as sediment is constantly settling from it into the water below. Currents of this type also cause fine-grained sediment to accumulate in preexisting depressions.

Calculations have been made as to the necessary amount of material in suspension to cause water of the densities now found on the shelf to flow to the bottom of the continental slope in the western North Atlantic. For near-shore water a minimum of 9.88 grams or 3.80 cc. per liter must be carried in summer and 3.29 grams or 1.17 cc. in winter. This presupposes an ideal condition wherein no additional sediment is picked up by acceleration and none lost by settling.

Seepage in the continental shelf, although not in itself capable of causing slumping of the material on the continental slope, may well be a contributory factor in the case of sediments whose equilibrium is unstable through other causes. The structure of the Coastal Plain, and presumably of its submerged extension, the continental shelf, covered as it is at its seaward margin by the unconsolidated silt and clay, is ideal for the operation of this process. Although the east-coast submarine canyons cannot have been produced by this means

alone, slumping and mud flows may have had important effects in further deepening pre-existing valleys.

The writers wish to acknowledge their debt to Messrs. C. O. Iselin of the Woods Hole Oceanographic Institution, and P. C. Rutledge of the Harvard Engineering School for suggestions concerning the quantitative data, and to Profs. R. A. Daly and P. E. Raymond for much helpful advice and criticism.

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SERUM PROTEIN MEASUREMENTS IN THE LOWER VERTEBRATES. II. IN MARINE TELEOSTS AND ELASMOBRANCHS

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The reasons for studying the plasma proteins of the lower vertebrates as shown in the first paper of this series (1) have to do with the validity of Starling's hypothesis for these forms and with the possible relation of the protein fraction of the plasma to nutritional needs. References to contributions in this field relating to the higher vertebrates will not be repeated. For the lower vertebrates, the list given by Drinker and Field (2) summarizes the information available up to their date of publication. A brief paper by Keys and Hill (3) gives the only findings for the colloid osmotic pressure of fish sera except those in two preliminary notes to this paper (4, 5). Interesting data allied in various ways are to be found in references (6) to (15) inclusive. The last two papers (14, 15) have excellent bibliographies.

The serum of various species of marine teleosts and elasmobranchs was studied at the Woods Hole Oceanographic Institution during the summers of 1933 and 1934, and during the summers of 1935 and 1936 at the Bergens Museum Biologiske Stasjon on the island of Herdla off the west coast of Norway. To both of these institutions most sincere thanks are due for the assistance generously rendered by them. A grant in 1936 from the Tracy McGregor Fund helped to defray expenses in that year.[2]

The determinations made were as follows: (1) colloid osmotic pressure, on all samples; (2) refractive index of the whole serum, on all samples; (3) refractive index on an ultrafiltrate, on many samples of the Norwegian series, whenever quantity of serum permitted; (4) total nitrogen and non-protein nitrogen in 1934, 1935, and 1936, a con-

[1] Contribution No. 148.

[2] The nitrogen determinations of the Woods Hole series were made by Catherine Goffin and those of the Norwegian series by Cand. mag. Francis Wolff, of Bergens Museum. Acknowledgment is made of the careful and helpful work done by both. At Woods Hole the Marine Biological Laboratory made its facilities available to Miss Goffin for her work; at Bergen the Norwegian Fiskeriforsöksstasjon allowed the use of its equipment for cold storage and for chemical work. Without this help it would have been impossible to make the nitrogen analyses.

siderable number of determinations, whenever quantity permitted. In all, 121 individual samples representing 19 species of teleosts were studied and 48 individual samples from 11 species of elasmobranchs. A few of these samples were assembled from two or more small fish each. There were in addition some scattered determinations on other species.

Methods

Obtaining the Fish

The fish whose blood is to be studied should be in a healthy condition and must be uninjured, to prevent access of the surrounding medium to the blood. To secure fish that meet these standards is difficult. The ordinary methods of fishing are extremely rough when viewed from the standpoint of obtaining true samples of the circulating blood. The effect of the severe struggling often incident to capture may not be negligible. Grafflin (8) has told in detail of his care in this matter of reliable sampling. The fish included in this study have been progressively better and none are included in the figures reported about which there is appreciable doubt. Two alternatives present themselves. Blood may be drawn the moment the fish is taken and this is for some species, for example those from deep water which will not live in tanks, the only possible method; or the fish may be allowed to rest for some hours or longer in cars or tanks of water suitable in temperature and aeration. Feeding is possible in some cases where the fish live well in captivity. The effect of the initial struggling is thus eliminated and the state of the fish is steadier. At least four of the most consistent sets of determinations in this study have been made mainly on fish thus treated, *Opsanus tau*, *Tautoga onitis*, *Anarhichas lupus*, and *Raia erinacea*. In certain species the skin is so delicate that it is probably best not to use them in such studies as these unless unusual care can be taken. It is possible that the two pleuronectids in the Woods Hole series belong in this group.

Enough is known about the relation existing between the blood and tissues of fishes and the demands of the breeding season to make avoidance of this period desirable in a preliminary survey. However, the length of this season is often far beyond the months mentioned in books so that it has not always been possible to avoid it without sacrificing the use of fish otherwise very suitable. The depression in the breeding season well-known to trout hatchery men, when the fish will eat nothing or very little, is of indeterminate length and not easily avoided. The breeding fish used in this series are so described. When it is not mentioned that a species was apparently ripe it is to be understood that as far as known the samples were not from breeding fish.

Blood Sampling

The blood was taken in 1933 by syringe from gill vessels or heart; in the other three summers, in most cases from tail vessels, occasionally from the heart. For the suggestion of taking blood from the tail, the author is indebted to Dr. Homer W. Smith. The fish is wrapped in a cloth, laid in a deeply grooved board, ventral side up, restrained by lacing tapes across the board, and held by an assistant. The syringe needle is inserted in the mid-ventral line, somewhat behind the anus, often along the anal fin, at an angle which will take it between the hæmal spines. It is pushed in until the vertebral column is felt, is slightly withdrawn and pushed in again quickly, with a good chance of puncturing a tail vessel from which blood can be withdrawn with a minimum of injury and a maximum of ease. If the tail vessels are too small for use or are covered by too firm a membrane between the spines, the heart is exposed, the ventral aorta clamped off by a hemostat, and blood withdrawn from the bulbus or venous sinuses. The blood must be handled gently when discharged from the syringe into the centrifuge tubes else hemolysis may occur. The same thing may happen if the vessel used is not entered quickly and neatly. Heparin has been used in both syringe and centrifuge tubes, but some clotting is usually evident after centrifuging, hence the term serum has been thought more appropriate than plasma.

The blood was centrifuged three or four hours after being withdrawn, not earlier because in that case delayed and repeated clotting sometimes occurs and is very troublesome if in osmometer tubes. After centrifuging, the serum was set up at once in the osmometers or kept in a very cold refrigerator until next day. Because it was impossible in Norway to have the nitrogen determinations made on the first day, various preservatives were tried, but all resulted in the appearance of a precipitate. Serum kept at about 0° C., on the other hand, remains clear for a period up to at least three weeks, and refractometric measurements show little or no alteration. At rather low room temperatures, 16°–19° C., osmometers containing teleost serum have held steady as long as three days. In the case of elasmobranch blood, the occasional rather warm intervals at Woods Hole, with room temperatures up to 25°, in a few instances caused the appearance of a thin whitish film on the membrane in the osmometer, but the colloid osmotic pressure in these cases seldom varied from the usual range. These films were not seen at the temperature of the Herdla laboratory, usually 15°–18° C.

A sterile technique was not attempted. The place where the needle was to be pushed through the skin was carefully wiped with

cotton. Syringes, needles, centrifuge and transfer tubes, and all other parts of apparatus coming into contact with the serum were cleaned systematically as follows. They were washed thoroughly with water, with soap when needed; they were rinsed thoroughly first with tap water, then with distilled water, finally with 70 per cent alcohol; they were dried in an oven at 70°–80° C. Contamination was not apparent except in the elasmobranch samples of the Woods Hole series in the hottest weather.

In general, then, while the securing, care, and preservation of the blood have presented difficulties, the samples included in this report

TABLE I

Protein determinations on serum of *Opsanus tau*, toadfish. Fish all of one lot, kept in aquarium up to 10 days, fed. One or two months after the breeding season. The length of the specimens varied from ten to twelve inches. Nos. 1 and 6 were females, the others males. C.O.P. Colloid osmotic pressure in mm. water pressure, determined from one or two osmometers. N-P. N. Non-protein nitrogen.

No.	Av. C.O.P.	Refractive index	Total N.	N-P. N.	Protein N.
	mm./water		*mg./cc.*	*mg./cc.*	*mg./cc.*
1	104	1.34401	—	—	—
2	119	1.34498	8.13	.866	7.26
3	76	1.34498	9.28	.809	8.47
4	100	1.34470	6.73	.494	6.24
5	95	1.34375	6.77	.497	6.27
6	127	1.34369	6.55	.419	6.13
7	125	1.34457	5.63	.423	5.21
8	111	1.34386	7.44	.368	7.07
9	97	1.34509	—	—	—
10	84	1.34468	—	—	—
Averages	*104*	*1.34443*	*7.22*	*.554*	*6.67*

are considered reasonably good. However, it is to be said that the history of the individual fish is in many important points entirely unknown. Its age, except as indicated roughly by its size, its recent activity when the fish has been bled immediately on being taken, its nutritive condition except that it may or may not have food in the digestive tract, all these factors of importance are not known. A considerable range in findings is to be expected.

The Identification of Species

The identification of species was made at Woods Hole by the use of Bigelow and Welsh (16) and in Norway by Otterström (17). In both places much help was received from various persons who know the

fishes of the region. Especial mention should be made of the Director at the Herdla laboratory, Professor August Brinkmann, and his son, and of the Assistant-Director, Dr. Rustad.

Methods of Testing

Colloid osmotic pressures were determined by the method of Krogh and Nakazawa (18) somewhat modified (19). The membrane used was cellophane no. 450. Refractive indices were determined by the dipping refractometers of Bausch and Lomb and Zeiss on both whole serum and its ultrafiltrate. The latter was secured from samples of

TABLE II

Protein determinations on serum of *Anarhichas lupus*, wolf-fish, 1935. Blood taken a few hours or a day after fish was brought to laboratory. Not near the breeding season. The length of the specimens varied from 18 to 30 inches. C.O.P. Colloid osmotic pressure in mm. water pressure. Derived from two to four osmometers in all cases except where only one osmometer was used, Fish No. 7. N-P. N. Non-protein nitrogen.

No.	Av. C.O.P.	n_D Serum	n_D Ultrafiltrate	n_D Colloid fraction	Total N.	N-P. N.	Prot. N.
	mm./water				*mg./cc.*	*mg./cc.*	*mg./cc.*
1	119	1.34530	1.33532	0.00998	6.15	.25	5.90
2	178	1.35588	1.33609	0.01979	10.94	.51	10.43
3	147	1.35051	1.33609	0.01442	7.96	.52	7.44
4	152	1.35128	1.33636	0.01492	8.55	.62	7.93
5	145	1.34702	1.33545	0.01157	8.12	.71	7.41
6	153	1.34832	1.33551	0.01281	—	—	—
7	150	1.34415	1.33551	0.00864	5.82	.77	5.05
8	177	1.34984	1.33578	0.01406	8.30	.77	7.53
Averages	*153*	*1.34916*	*1.33576*	*0.01328*	*7.98*	*.69*	*7.38*

the Norwegian series by a Thiessen apparatus, with care as to uniformity of technique. Two cubic centimeters of serum were placed in the apparatus with cellophane no. 450 as membrane and subjected to a pressure of some three atmospheres for a period of 12 hours. At the end of this time a clear, limpid filtrate was obtained, always protein-free. The residue on the membrane at this time was small in amount and slimy in character. Tests for chloride and reducing sugar showed them to be present in the ultrafiltrate. It was assumed that the membrane was permeable to practically all the serum crystalloids.

Nitrogen determinations were made in 1934 at Woods Hole by the micro-Kjeldahl method with direct Nesslerization. For the non-protein determinations the precipitant was trichloracetic acid. In

1935 and 1936 the micro-Kjeldahl method was by titration. The precipitant was metaphosphoric acid. All methods and reagents were suitably controlled and tested.

Table III

The colloid osmotic pressure of the sera of marine teleosts. Arranged in order of height of osmotic pressure, in two series.

Name of species	Number of individuals	C.O.P. Range	C.O.P. Average
		mm. water	*mm. water*
Woods Hole Series			
Sarda sarda, Bloch. Bonito	1	233	233
Echeneis naucrates, Lin. Remora*	1	216	216
Tautoga onitis, Lin. Tautog*	24	79–193	129
Paralichthys dentatus, Lin. Summer flounder			
Pseudopleuronectes Americanus, Wal. Winter flounder	6	79–180	120
Prionotus Carolinus, Lin. Common robin*	7	86–122	106
Prionotus strigatus, Cuv. & Val. Red-winged robin*	7	87–117	102
Opsanus tau, Lin. Toadfish	10	76–127	104
Norwegian Series			
Scomber scombrus, Lin. Mackerel	3 samples fr. 11 fish‡	164–212	198
Anguilla vulgaris, Tur. Eel	4 samples fr. 13 fish‡	167–204	189
Belone acus, Risso. Hornfish	2	162, 184	173
Anarhichas lupus, Lin. Wolf-fish	13	85–181	147
Brosmius brosme, Asc. Cusk†	8	105–210	139
Molva molva, Flem.†	4	108–177	139
Gadus morrhua, Lin. Cod	11	70–192	117
Gadus pollachius, Lin. Pollack	8 samples 3 fr. 6 fish‡	31–172	94
Cyclopterus lumpus, Lin. Lumpfish*	3	75–87	81
Lophius piscatorius, Lin. Goosefish	8	25–60	42
Gadus virens, Lin.	1 fr. 2 fish‡	40	40

* Breeding season.

† From deep trawl, 300–400 meters. Fish with swim-bladders protruding or burst and with organs extruded in some cases on arrival at surface. Blood samples taken immediately on board the collecting boat.

‡ Samples from more than one fish because of small size of samples available from single individuals. The refractive indices were found to be similar before samples were combined.

Results

The results of the study are presented in a series of annotated tables. The determinations on teleosts are given first. To show the range of variation among individuals of a single species *Opsanus tau*, Lin., toadfish, was chosen from the Woods Hole series of 1934, Table I,

and *Anarhichas lupus*, Lin., wolf-fish, Table II, from the Herdla series of 1935. The toadfish was chosen as a sluggish fish, much studied at Woods Hole laboratories, and the wolf-fish as a more vigorous species much studied in Norway.

TABLE IV

Refractive indices of sera and ultrafiltrates from marine teleosts. Arranged in order of height of C.O.P. Figures in parentheses indicate the number of individuals used for the following average, when this is less than the total number.

Name of species	Number of individuals	n_D Serum	n_D Ultrafiltrate	n_D Colloid
Woods Hole Series				
Sarda sarda	1	1.35220	—	—
Echeneis naucrates	2	1.35158	—	—
Tautoga onitis	24	1.34629	—	—
Paralichthys dentatus				
Pseudopleuronectes Americanus	6	1.34313	—	—
Prionotus Carolinus	7	1.34329	—	—
Prionotus strigatus	7	1.34205	—	—
Opsanus tau	10	1.34443	—	—
Norwegian Series				
Scomber scombrus	3 samples fr. 11 fish*	1.35000	(2)1.33690	0.01306
Anguilla vulgaris	4 samples fr. 13 fish*	1.35152	1.33552	0.01600
Belone acus	2	1.35084	1.33724†	0.01360
Anarhichas lupus	13	1.34852	1.33577	0.01275
Brosmius brosme	5	1.34703	1.33574	0.01169
Molva molva	4	1.34597	(2)1.33601	0.00912
Gadus morrhua	11	1.34421	1.33588	0.00834
Gadus pollachius	8	1.34401	1.33594	0.00807
	3 of these fr. 6 fish*			
Cyclopterus lumpus	3	1.34388	1.33535	0.00853
Lophius piscatorius	8	1.34168	1.33545	0.00623
Gadus virens	1 sample fr. 2 fish*	1.34158	1.33559	0.00599

* See note on Table III.

† Samples used for obtaining ultrafiltrates in these cases were only one cubic centimeter instead of two as usual. This may explain the aberrant value.

Table III summarizes the data on colloid osmotic pressure from the teleosts of Woods Hole and Herdla; Table IV, the data on refractive indices; Table V, the nitrogen determinations. The fish from Woods Hole and Herdla are listed separately, since the procedures were more complete in the later series. The order of names in all tables is that of the relative heights of the colloid osmotic pressure, even though the

order of refractive indices and of nitrogen content does not follow exactly the same course.

In a similar manner Tables VI–IX present the data for elasmobranchs, Table VI showing the variation among individuals of a single species, *Raia erinacea*, Lin., small skate, and Tables VII–IX the colloid osmotic pressure, refractive indices, and nitrogen findings respectively for the several species of elasmobranchs.

An effort was made to study *Myxine glutinosa*, Lin., hagfish, but it

TABLE V

Nitrogen determinations on sera of marine teleosts.

Name of species	Number of individuals	Total N.	N-P. N.	Protein N.
		mg./cc.	*mg./cc.*	*mg./cc.*
Woods Hole Series				
Echeneis naucrates	1	6.68	.272	6.41
Tautoga onitis	6	6.62	.498	6.12
Paralichthys dentatus				
Pseudopleuronectes Americanus	3	5.48	.452	5.03
Prionotus Carolinus	1	7.90	.747	7.15
Opsanus tau	7	7.22	.554	6.67
Norwegian Series				
Scomber scombrus	2 samples fr. 9 fish*	8.30	.65	7.66
Anguilla vulgaris	3 samples fr. 11 fish*	8.47	1.19	7.28
Anarhichas lupus	10	8.11	.70	7.48
Brosmius brosme	1	6.95	.57	6.38
Gadus morrhua	5	5.93	.60	5.33
Gadus pollachius	3 samples fr. 5 fish*	6.11	.76	5.34
Cyclopterus lumpus	3	5.37	.25	5.09
Lophius piscatorius	8	4.85	.44	4.41
Gadus virens	1 sample fr. 2 fish*	3.99	.39	3.60

* See Table III.

was found very difficult to secure blood samples entirely uncontaminated by slime. The individuals were not large enough to yield more than about one cubic centimeter of blood, often less, and therefore of necessity the determinations were made on mixed samples, though the refractive indices were taken before mixing and only samples of similar indices combined. From one such mixed sample two osmometers gave an average of 24 mm. c.o.p., the total serum showed a n_D of 1.35073, the ultrafiltrate n_D 1.33923, thus giving a colloid index of 0.01150. The total N of the serum was 5.88 mgm./cc.

Table VI

Protein determinations on serum of elasmobranch, *Raia erinacea*, small skate. Fish of different lots, kept in aquarium not more than three or four days. Height of breeding season, several eggs laid in aquarium. The length of the specimens varied from 17 to 19 inches. Nos. 2, 3 and 9 were males, the rest females.

C.O.P. Colloid osmotic pressure, determined from one to three osmometers, usually two.

N-P. N. Non-protein nitrogen.

No.	Av. C.O.P.	Refractive index	Total N.	N-P. N.	Protein N.
	mm./water		*mg./cc.*	*mg./cc.*	*mg./cc.*
1	63	1.34694	16.83	—	—
2	73	1.34886	16.95	—	—
3	14	1.34665	—	—	—
4	50	1.34581	—	—	—
5	47	1.34895	—	—	—
6	71	1.34765	—	—	—
7	17	1.34661	15.91	—	—
8	16	1.34661	14.78	13.55	1.23
9	14	1.34849	13.13	13.02	0.11
10	34	1.34683	16.39	13.19	3.20
11	19	1.34618	16.39	13.71	2.68
12	29	1.34640	16.75	13.88	2.87
Averages	*37*	*1.34715*	*15.49*†	*13.47*†	*2.02*†

† Five only used for average.

Table VII

The colloid osmotic pressure of the sera of elasmobranchs, arranged in the order of the height of the osmotic pressures.

C.O.P. Colloid osmotic pressure.

Name of species	Number of individuals	C.O.P. Range	C.O.P. Average
		mm./water	*mm./water*
Woods Hole Series			
Carcharias taurus, Raf. (sp.?) Shark	1	46	46
Mustelus canis, Mitch.† Smooth Dogfish	4	33–58	41
Raia erinacea, Mitch.† Small Skate	12	14–73	37
Dasybatus marinus, Klein. Stingaree	1	36	36
Norwegian Series			
Raia fullonica, Lin.‡	2	14, 49	32
Chimæra monstrosa, Lin.‡	5	10–40	27
Galeus vulgaris, Flem. Shark	1	27	27
Squalus acanthias, Lin.‡ Spiny Dogfish	2	23, 31	27
Pristiurus catulus, Gun.‡	7	5–59	26
Raia oxyrhynchus, Lin.† ‡	6	11–45	22
Etmopteris spinax, Lin.† ‡	7 samples fr. 14 fish*	–8–34	17

* Individual fish small, about 12–14 inches. Samples were therefore combined, but only after refractive indices had shown them to be in the same range. Two negative values may indicate the error of the method when the pressure is extremely low.

† Breeding season.

‡ From deep trawl, 300–400 meters. No outward sign of injury on coming to the surface. *E. spinax* and *R. fullonica* lived often as long as 24 hours in laboratory tanks.

Table VIII

Refractive indices of sera and ultrafiltrates from elasmobranchs. The number in parentheses (4) indicates that the following n_D was derived from 4 individuals only. See notes on Table VII.

Name of species	Number of individuals	n_D Serum	n_D Ultra-filtrate	n_D Colloid
Woods Hole Series				
Carcharias taurus	1	1.34601	—	—
Mustelus canis†	4	1.34618	—	—
Raia erinacea†	12	1.34715	—	—
Dasybatus marinus	1	1.34682	—	—
Norwegian Series				
Raia fullonica‡	2	1.34852	1.34079	0.00774
Chimæra monstrosa‡	5	1.34596	(4) 1.34063	0.00486
Galeus vulgaris	1	1.34422	1.34113	0.00309
Squalus acanthias‡	1	1.34671	1.34096	0.00575
Pristiurus catulus‡	7	1.34423	1.34076	0.00331
Raia oxyrhynchus† ‡	5	1.34412	1.34070	0.00342
Etmopteris spinax† ‡	7 samples fr. 14 fish*	1.34353	1.34055	0.00288

the N-P.N., 0.22 mgm./cc. These figures do not seem concordant, but are reported since data on this form are few.

Body fluid was present in one instance only in quantity sufficient for collection and study. This was in a wolf-fish of medium size and

Table IX

Nitrogen determinations on sera of elasmobranchs. See notes on Table VII. Number in parentheses (1) indicates that in only one instance was there serum enough for the determination of the N-P. N.

Name of species	Number of individuals	Total N	N-P. N.	Protein N.
		mg./cc.	*mg./cc.*	*mg./cc.*
Woods Hole Series				
Raia erinacea†	5	15.49	13.47	2.02
Dasybatus marinus	1	16.85	11.81	5.04
Norwegian Series				
Raia fullonica‡	3	17.50	12.16	5.34
Chimæra monstrosa‡	1	13.91	11.15	2.76
Galeus vulgaris	1	13.76	11.47	2.29
Squalus acanthias‡	1	14.98	12.68	2.30
Pristiurus catulus‡	3	12.72	9.58	3.14
Raia oxyrhynchus† ‡	6	15.07	12.31	2.76
Etmopteris spinax† ‡	4 samples fr. 5 fish*	12.18	(1 10.07	1.60

medium serum values. There was nothing to indicate that the fish was not in a healthy condition. The data are given in Table X. The body fluid showed a c.o.p. nearly four-fifths that of the serum, and while the refractive index did not show quite as high a colloid fraction, yet it is clear that this fluid contained a considerable amount of protein, an amount comparable to that found in the body fluid of the "slider" turtle (1).

Discussion of Results

Regarding the results on teleosts, it is apparent that the findings for a single species show a range proportionately wider that we expect in mammals. Such a lack of constancy has been found by other workers on fish blood. (See references in the first paragraph of this paper.) Whether this is really true or due, in spite of efforts to the contrary, to the use of unsuitable specimens is not known. Studies are in progress on fresh-water species living in the controlled environ-

Table X

Comparison of serum and body fluid from one specimen of *Anarhichas lupus* from which enough body fluid was obtainable for colloid osmotic pressure and refractometer tests though not for nitrogen analyses.

Fluid	C.O.P.	n_D Serum or fluid	n_D Ultrafiltrate	n_D Colloid
	mm./water			
Blood serum	129	1.34707	1.33563	0.01144
Body fluid	98	1.34184	1.33532	0.00652

ment of fish hatchery ponds to see if the variation from individual to individual is as great as that seen in the toadfish, 76–127 mm. or in the wolf-fish, 119–178 mm. water pressure. Also the yearly rhythm is being followed to see whether colloid osmotic pressure shows the effect of elaboration of sex products and of spawning depression.

There is obviously a wide difference between the colloid osmotic pressure of the goosefish, 42 mm. and that of the mackerel, 198 mm. This latter value is similar to that found by Keys and Hill (3) for *Anguilla*, the European eel, and verified in this series. The ranges for individuals of these species are seen to be mutually exclusive, but those for species nearer the middle of the total range overlap freely and some are indistinguishable, as for instance the two species of *Prionotus*. To what this characteristic range for a species is related is not known though various suggestions have been made. Arterial pressure determinations on fish are few and reliable determinations still fewer (20), while determinations of capillary pressure have not been

made at all. The degree of habitual activity has been suggested as a clue, for *Lophius* is proverbially sluggish and *Scomber* very active, while the extensive migrations of *Anguilla* are well-known. The series is as

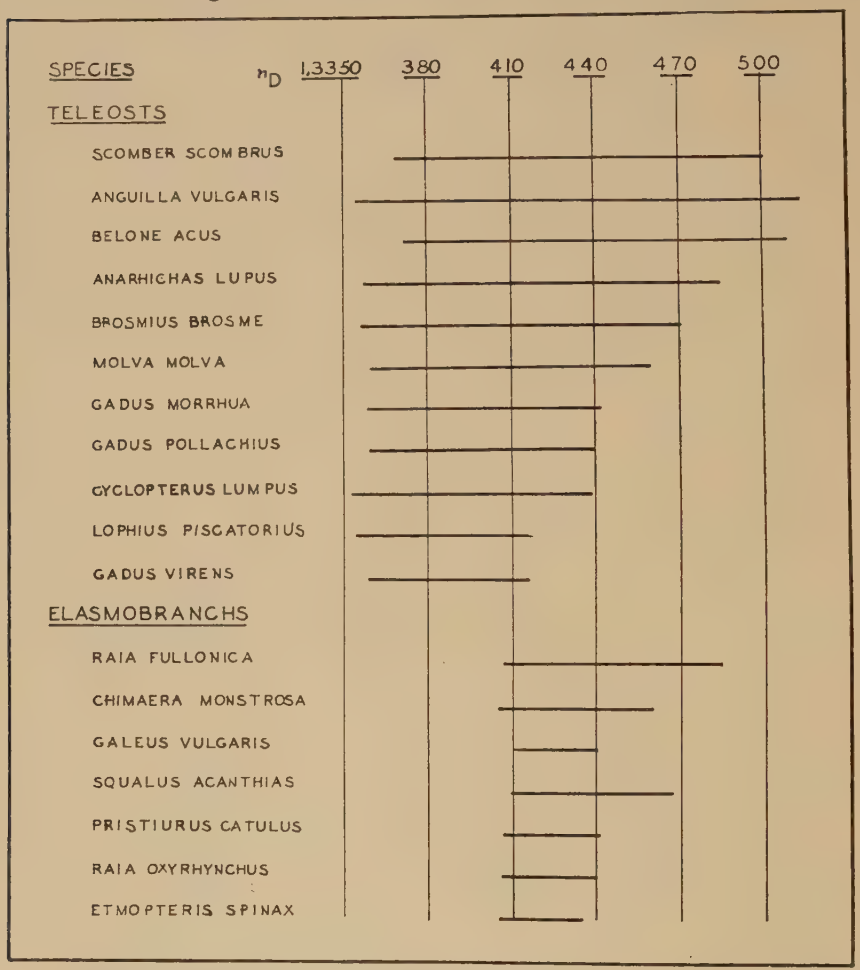

CHART 1. Refractive indices of colloid fraction in Norwegian series of teleosts and elasmobranchs. The left end of each line shows the refractive index of the ultrafiltrate, the right end that of the whole serum. The length of the line therefore shows the index of the colloid fraction. The ultrafiltrates in all of the teleosts except two are closely grouped, indicating relative constancy in the non-colloid components of the sera. The two exceptions are in fish which were represented by limited samples only, in the case of Belone by samples for ultrafiltration of only half the usual size. The high position of the ultrafiltrate index for all elasmobranchs is related to their high non-protein nitrogen fraction.

yet too short to give an answer here. The possibility of other substances which may add to the colloid osmotic pressure of the serum, e.g. fats (21, 22) is not to be excluded particularly when one occasion-

ally sees globules of fat at the top of a centrifuged tube of blood and infers the presence of associated substances in solution in appreciable amounts. Also the wide variation in the fat content of fish is a matter of common knowledge. No determinations on serum fats have been made. The albumin-globulin ratios in fish are said by Lepkovsky

CHART 2. Comparison of colloid osmotic pressure, refractive index of colloid fraction, and protein nitrogen in Norwegian teleost series. The several ranges have been adjusted so that the maximum values are shown by lines of approximately equal length. The relative values of the three measurements thus appear, with a range much wider in c.o.p. than in n_D or protein N. This is probably to be explained by a variation in the albumin-globulin ratio in the direction of large molecules when the total quantity is small.

(11) to vary widely. Such variations, with their attendant contrast in the size of the protein molecules, may help to explain not only differences between species but irregularities in the relationships between colloid osmotic pressure and other protein data. A few preliminary studies on plasma protein regeneration after depletion by

hemorrhage seem to indicate that protein may come back rather quickly, perhaps more quickly in total quantity than in colloid osmotic pressure, which may be the same as saying that the globulins regenerate—or are gotten into the blood—more rapidly than the albumins. This obviously suggests the experiments on mammalian protein regeneration from the laboratories of Whipple and Weech, to whose papers only partial references are given (23, 24, 25).

As the refractive indices are scrutinized, it is apparent that the range for the ultrafiltrates is narrow, indicating constancy in the non-protein fraction of the plasma, while the refractive index for the colloid fraction varies widely from species to species and accompanies the c.o.p. though the correspondence is not too close. (See Chart 1.) The analyses for total and non-protein nitrogen similarly give values for the serum proteins which vary approximately with the c.o.p. but follow more closely the refractive indices of the colloid fractions. These correspondences and differences are brought out in Chart 2. It is to be noted that the range of c.o.p. from the species of low to those of high values is much greater than the range in protein content. This fact may be associated with the ready appearance of protein molecules of large size mentioned above. It is possible that in the life economy of teleosts it is of especial importance to hold the total protein content of the serum at a definite level while the assortment of proteins may vary. It would follow from this that a rigid maintenance of colloid osmotic pressure is impossible or unnecessary.

For the elasmobranchs it is to be said that all averages for colloid osmotic pressure are low, though occasional individuals have been found as high as 70 mm. water pressure. As expected, the total and non-protein nitrogen findings, the refractive indices for total sera and for ultrafiltrates are all high, reflecting the high urea or trimethylamine oxide content of elasmobranch blood. The protein nitrogen figures are low with two exceptions, one specimen of *Dasybatus marinus*, stingray, and three of *Raia fullonica*, a Norwegian skate. Differences in the physiological make-up of elasmobranchs and teleosts thus include the protein blood picture.

Summary and Conclusions

1. In a study of 121 individuals of 19 species of marine teleosts it has been found that the range of colloid osmotic pressure shown by the blood serum is wide for a single species; that the c.o.p. shows a characteristic range in each species; and that for the species studied the c.o.p. varies from an average of 42 mm. water pressure in *Lophius piscatorius*, Lin., goosefish, to about 200 mm. in *Scomber scombrus*,

Lin., mackerel, *Anguilla vulgaris*, Tur., eel, and probably others. Intermediate values for averages within species were found most commonly, from about 100 to 150 mm.

2. The refractive indices for the colloid fractions of the sera and the protein nitrogen values follow the same general distribution as the c.o.p. though correspondence is not perfect. The c.o.p. seems to vary through a much wider range than the protein N or the refractive index of the colloid fraction.

3. All protein values for the 48 individuals of 11 species of elasmobranchs were found to be low, distinctly lower than in all save the very lowest of the teleosts.

4. The refractive indices of the ultrafiltrates from the sera in all teleosts were very constant as compared with the wide range of the colloid figures. This constancy, reflecting the crystalloid status of the sera, is also characteristic of the elasmobranch ultrafiltrates though the absolute level is materially higher in the latter group, a fact associated obviously with the high non-protein nitrogen content of elasmobranch blood.

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Contribution No. 149

ON THE LONGITUDINAL VARIATIONS IN THE DYNAMIC ELEVATION OF THE SURFACE OF THE CARIBBEAN CURRENT*

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In a report on the hydrography of the Central American Seas the author has pointed out that the Caribbean Current must ascend a considerable calculated dynamic slope on the passage from the eastern end of the Caribbean to the Cyaman Sea. In the accompanying Figure 1, the topographic complications of the Caribbean and Cayman Seas are illustrated by the 100-fathom contour lines. For our study in relation to topography, the probable general features of horizontal ciriculation have also been entered according to Parr, 1937, fig. 53. Figure 2 presents the dynamic topography of the surface in relation to 1200 decibars, from which the impossibility of drawing any path of flow without apparent dynamic ascent in the empirically known direction of the current from the southeast to the Cayman Sea is obvious. Figure 3 shows the general trend of longitudinal dynamic slopes and longitudinal vertical distributions of temperatures and salinities in the upper 1000 meters in the path of the current, based upon the averages for the 1–4 stations of each transverse profile located in or adjacent to the path of the main current from the southern part of the Lesser Antilles to the Yucatan Channel as shown in Figure 1. Below the dynamic and hydrographic profiles, Figure 3 also shows a bottom profile on a reduced vertical scale. The heavy line indicates average bottom profile while minor banks or lateral ridges are indicated in varying degrees of lighter solid or broken lines, according to their transverse extent and their proximity to the current ribbon on which the longitudinal hydrographic profile is based.

From the upper part of Figure 3 we see that there is a steady increase in dynamic elevation of the surface of the Caribbean Current in a downstream direction. It is evident, of course, that this increase in dynamic elevation of the surface is simply a cumulative expression of an increase in the thickness of the upper layers of lower densities. This increase is shown in the temperature and salinity profile below the dynamic profile of the surface. It is further obvious from both

*Joint Contribution from Woods Hole Oceanographic Institution (No. 149) and Bingham Oceanographic Foundation, Yale University.

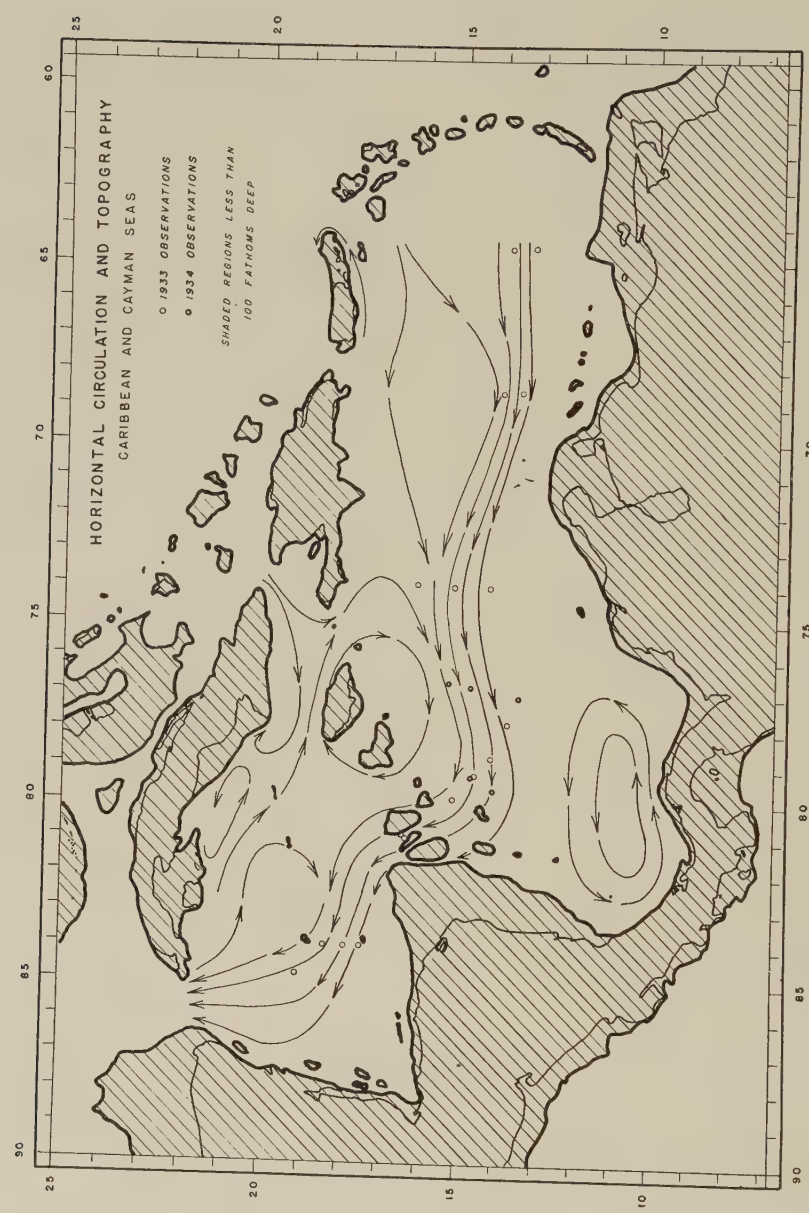

Figure 1. Topography and general horizontal circulation. Caribbean and Cayman Seas. Land masses above 100 fathoms depth shaded.

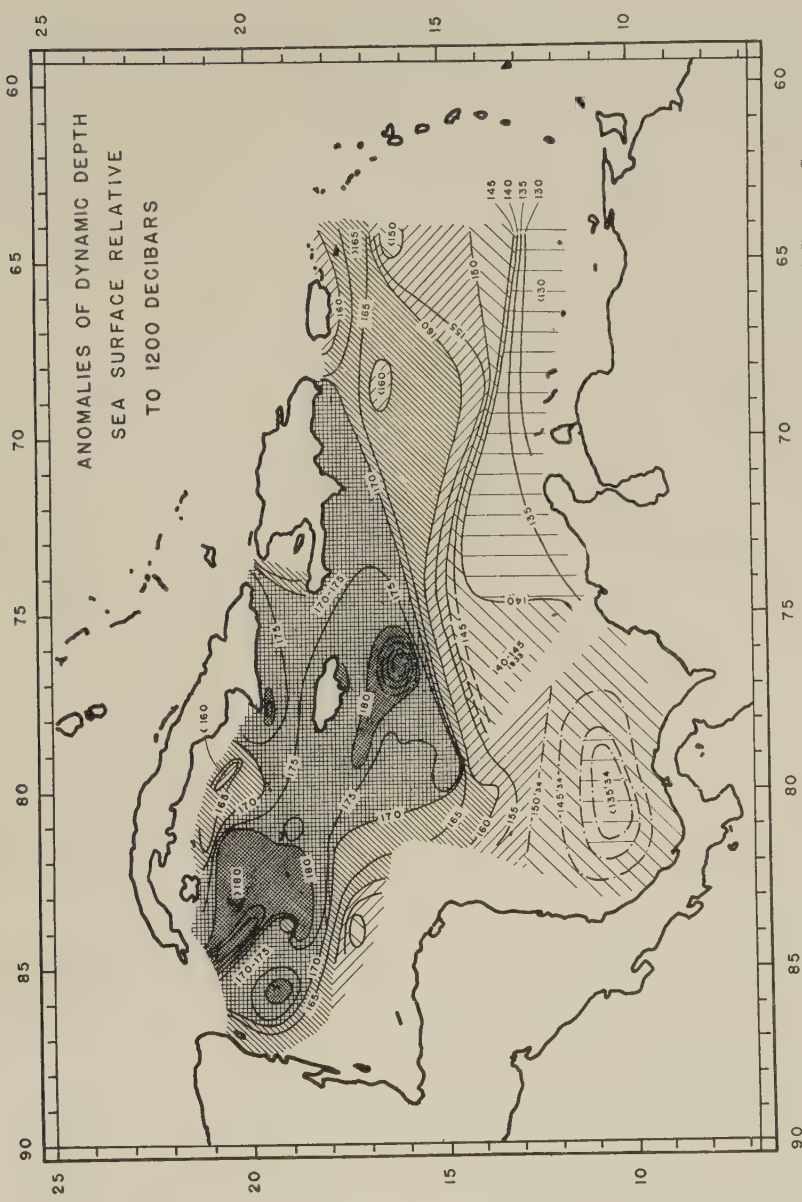

Figure 2. Dynamic topography of surface relative to 1200 decibars. Caribbean and Cayman Seas.

profiles that there are two patterns superimposed upon each other in this longitudinal variation, both in the dynamic surface gradient and in the vertical distributions. Firstly, there is a very obvious general slope downward in the direction of flow of all the upper isotherms and isohalines with a corresponding general rise in the dynamic elevation of the surface. Secondly, there are some very conspicuous deviations from these general trends to be observed in strict correlation with the variations in topography. Each subordinate pattern has probably, as we shall see, an entirely distinct explanation and can therefore be discussed separately.

It might be added at this point that undulations in the dynamic profiles similar to those observed over the Jamaica-Honduras ridge also occur in the passage over the Yucatan Channel threshold; but since the proximity of the main current to the left shore in the Yucatan Channel makes rather extensive interpolations of dynamic height over sloping bottom necessary in this locality, with consequently increased uncertainty about the exact values, the region of the Yucatan Channel has not been included in Figures 2 and 3. The average anomaly of dynamic height of the surface relative to 1200 decibars across the entire Yucatan Channel profile is about 170 dyn. cms., but if we consider only the western half as the path of the main current, the surface of the latter would have an average anomaly of dynamic height relative to 1200 decibars of only about 150 dyn. cms. Interpolations over the Jamaica-Honduras ridge are also very complicated and difficult, and it is quite possible that the dip in the profile at this point should be even deeper than shown in Figure 3, where the curves are only indicated by dots and dash through this region in accordance with this uncertainty.

Before proceeding with the discussion of probable causes and explanations, however, we should mention the fact that an extension of our calculations to levels below the 1200 decibar surface shows only the absolute impossibility of finding a compensating slope of the 1200 decibar surface in relation to greater depth by standard methods of observation and calculation. The maximum range of calculated variations in dynamic thickness between 1200 decibars and 3000 decibars is only 10.2 dynamic centimeters. These variations might thus account for one-third to one-fourth of the longitudinal slope calculated with reference to the 1200 decibar surface (30–40 dyn. cm.), if they were distributed horizontally in such a fashion as to produce a com-

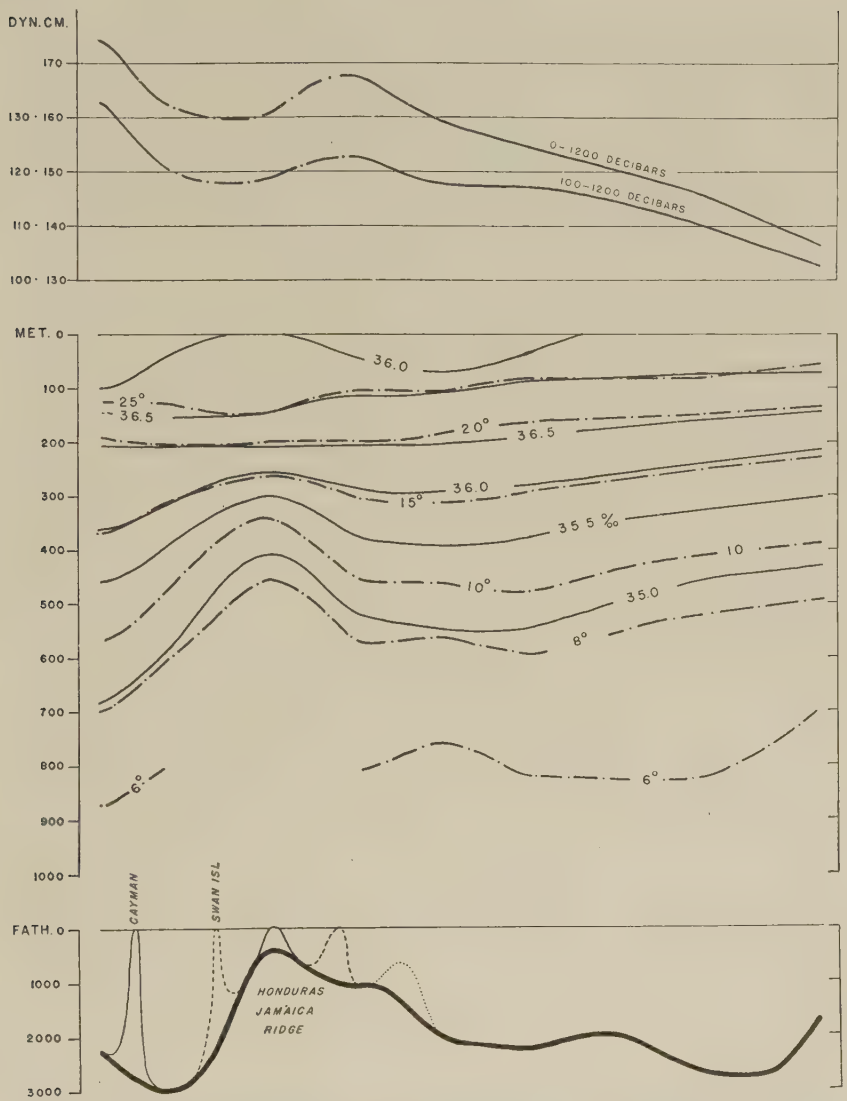

Figure 3. Longitudinal profiles of Carribbean current. *Top:* Anomalies of dynamic height in cm. relative to 1200 decibars in Caribbean current. *Centre;* Salinities and temperatures. Depth in meters. *Bottom:* Bottom profile. Depths in fathoms.

pensation for the slope observed in the upper water masses. This, however, is not the case. The variations in dynamic thickness between 1200 and 3000 decibars are quite irregularly distributed, and that they do not compensate for the longitudinal increase in dynamic thickness between surface and 1200 decibars can be definitely shown by a comparison between averages for the Caribbean and for the Cayman Sea (comp. fig. 2). When we take the averages for 30 stations in the Caribbean with depths extending low enough to make hydrodynamic calculations down to the 3000 decibar surface and compare them with 13 stations in the Cayman Sea where similar data are available, we find that there is an increase in average dynamic thickness between surface and 1200 decibars as we proceed from the Caribbean to the Cayman Sea of 26.88 dyn. cm. (from 148.27 dyn. cm. to 175.15 dyn. cm.), while the averages of dynamic thickness between 1200 decibars and 3000 decibars only show a decrease of 0.33 dyn. cm. (from 96.88 dyn. cm. in the Caribbean to 96.55 dyn. cm. in the Cayman Sea.) The ratio of the differences in longitudinal change of dynamic thickness between surface and 1200 as compared with 1200 to 3000 decibars is thus only of the magnitude of 1:81.7, that is, the calculable variations in dynamic thickness between 1200 and 3000 decibars can only on an average account for one eighty-secondth of the calculated increase in dynamic thickness between 1200 decibars and the surface. At 3000 decibars we are below all external as well as internal threshhold levels. To look for any compensation in the water masses below 3000 decibars is therefore obviously out of the question. This is also shown by the great uniformity of the water masses found in the bottoms of the Central American Basins (see Parr 1937, pp. 48–52).

That some of the longitudinal increase in dynamic elevation may be a function of time through the progression of vernal heating is obvious. But even if we allow the patently exaggerated assumption that the entire increase in dynamic thickness of the upper hundred meters could be credited to this effect alone, and consider only the increase between 100 and 1200 decibars, we still obtain a picture quite similar to that shown by the surface itself in relation to 1200 decibars (see figure 13). It is therefore obvious that vernal heating can at most only account for a very small fraction of the longitudinal variations observed.

It is thus evident that *the calculated longitudinal increase in dynamic height is not due to the manner of application of the dynamic method but*

is an unavoidable result of the method itself. If the result should not be in accordance with the actual, but unknown, distribution of pressures, this, therefore, only means that inherent limitations of the method makes it inapplicable to conditions such as those with which we are here dealing. The reasons why the method may become inapplicable under such conditions, and the conclusions which may be reached from this very fact, are therefore the subject of discussion in this article.

Considering first the general trend of progressive thickening of a upper layers downstream as expressed by the deepening of the isotherms and isohalines and by the increasing relative dynamic elevation of the surface, we realize that this phenomenon may quite possibly be due to the fact that being in a steady trade-wind region the Caribbean Current is accelerated constantly from the surface in its passage through the waters with which we are dealing. It therefore seems necessary to attempt to analyze the possible effects of acceleration from above upon the vertical distribution of velocities and trajectories under more simple abstract circumstances and to see how far our conclusions may then be found to be in accordance with the observed features of the Caribbean Current. While the quantitative analysis must be left to the dynamicists, the author would nevertheless venture to suggest some qualitative considerations by which a first approach to the solution of the problem may possibly be made.

If we consider the flow of a liquid through a channel of uniform width in which it is subject to acceleration from above while lateral expansion or contraction is excluded, and in which for simplicity's sake we may also assume the absence of skin friction and therefore also the absence of any transverse velocity gradients, a number of different situations are conceivable and capable of qualitative analysis.

1. The channel is assumed to have a level and rigid bottom at a finite depth (D) and the liquid, which is entirely homogeneous throughout, enters the channel with a rectilinear distribution of velocities from surface to bottom. If acceleration from the surface occurs, e. g. by winds blowing in the same direction as the flow of the current, it is obvious from the continuity principle that there must be a convergence upward of the upper mean trajectories (fig. 4A), since the average velocity u_1 in the upper part of the column H_1 after (*during*) acceleration must be greater than the average velocity v_1 in the upper part of the column D_1 above the corresponding trajectory before acceleration. Since the mass transport must remain the same, that is,

$$H_1u_1 = D_1v_1 \qquad \text{and } u_1 > v_1$$

it follows that: $H_1 < D_1$

If we introduce an arbitrary symbol $\delta\,\overline{d}$ (trajectory depth differential) we may generalize this in the statement:

$$v\ \delta\,\overline{d} = \text{constant}$$

The continuity principle, however, also applies to the entire thickening of the moving liquid as well as to the fraction of the liquid contained between the surface and any particular intermediate trajectory. Therefore, since an equal mass transport must occur in the *decreasing* depth between the surface and some upper trajectory, the same must also be true of the mass transport in the *increasing* depth between this trajectory and the rigid bottom. We thus have

$$H_2u_2 = D_2v_2$$
$$H_2 > D_2$$

and therefore: $u_2 < v_2$

That is, *acceleration from above must actually reduce the average velocity of the entire column below* (*exclusive of*) *the infinitesimal surface integral itself* since it is evident (see fig. 4A) that the above reasoning applies to a comparison between the liquid above and below any particular trajectory whatsoever below the very surface itself. According to the same reasoning, acceleration from above must also increase the average velocity above (exclusive of) the infinitesimal bottom integral (but inclusive of the surface integral). Acceleration from above must therefore change the vertical velocity distribution in some such manner as that indicated in Figure 4B. That is to say, acceleration increases average velocity above and reduces average velocity below any level whatsoever between the surface and the bottom, while the average velocity of the entire column must remain unchanged, with the acceleration only expressed in an increase in the momentum transport:

$$\int_{\text{Bottom}}^{\text{Surface}} Mv^2$$

but not in the mass transport

$$\int_{\text{Bottom}}^{\text{Surface}} Mv$$

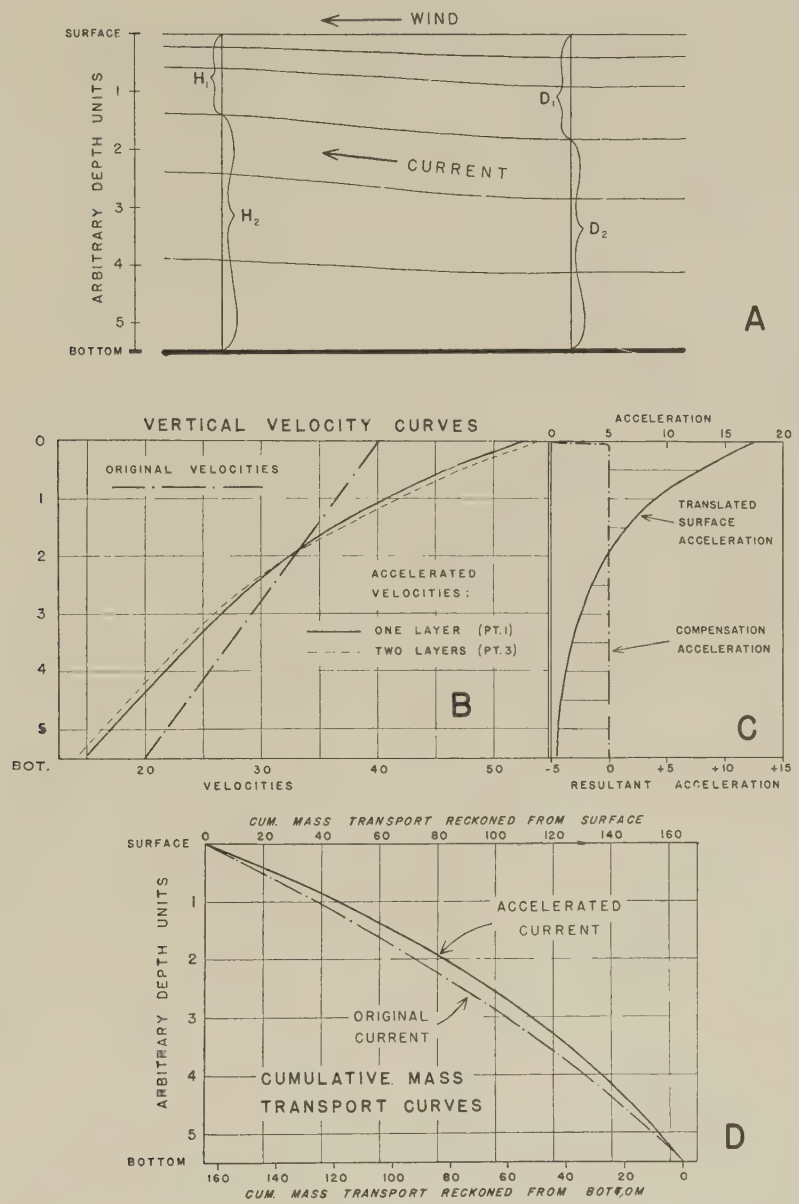

Figure 4. See text.

The velocity curves shown in Figure 4B give about 12% increase in momentum transport by acceleration, but no change in mass transport according to the continuity principle.

In terms of particular velocities at any special level, however, we see from Figure 4B that these may be either increased or reduced by acceleration, depending upon whether the level considered is situated above or below the intercept between the original and the accelerated particular velocity curve (fig. 4C). But the important point remains that *not only the average velocities below a certain level, but also the particular velocities in the deeper levels and along the deeper trajectories must suffer actual retardation by acceleration of the entire water-mass from above.* We must therefore look for a retarding mechanism for the deeper layers directly induced by the acceleration of the upper water-mass.

As a simplifying mathematical fiction we may consider the retardation of the lower trajectories as a current in the opposite direction identified by negative velocities in the system under consideration. Since the necessity for this negative current arises from the continuity principle, it is obvious that we are actually quite simply dealing with a compensation current and that the actual flow represents the algebraic sum of this compensation current and the gradient or wind-drift movement. What we are looking for is therefore the mechanism of a compensation flow.

Since we are dealing with an homogeneous liquid, it is evident that the vertical changes in trajectories will not alter the uniform distribution of pressures along the bottom so long as the free surface remains horizontal. Acceleration from above must therefore depress the surface itself in the upstream direction, thereby producing a relative increase in pressures downstream which serves to create the negative compensation current, or retardation, below the accelerated surface layer. This, in other words, merely expresses the commonsense conclusion that a compensation movement cannot be generated until some water has actually been removed so as to create the need for such compensation.

Since the water is homogeneous, the upstream dynamic gradient of the compensation current is uniform throughout the entire liquid depth.* The upstream acceleration of the compensation movement

* Below the deepest level of the depression, which is so slight that it can be disregarded.

is therefore also uniform in the vertical (fig. 4C) while the translated acceleration from above, of course, decreases towards the depths. Since the resultant effect upon the flow is the algebraic sum of the compensation acceleration and the translated wind acceleration, the effect must be in the nature of acceleration above the intercept between the translated surface acceleration curve and the compensation acceleration curve, and must take the form of a retardation below this intercept, as suggested in Figure 4C. From this figure and from the above considerations, it is now evident that the resultant retardation in the homogeneous liquid must have its maximum at the bottom itself, that is, there must be an inherent tendency to expand downwards also in the bottom layer which is merely kept in check by the rigidity of the bottom itself. Therefore:

2. If the homogeneous water considered under point *1* (above) before acceleration were only moving over a horizontal liquid boundary at the same depth (D) as that of the rigid bottom assumed under point *1* and conditions were otherwise the same, acceleration from above should serve to depress this boundary in the downstream direction. If the layer below is of greater specific density, the depression of the boundary with acceleration must now introduce a progressive reversal of the dynamic gradient of the compensation movement towards deeper levels, since heavier water will now occur at higher levels upstream (fig. 5).

Below the deepest depression of the liquid boundary horizontal isobaric surfaces may now again develop. At some still greater depth it might also be possible to find a horizontal level which was both *isobaric, isopycnal,* and *limiting of a uniform mass transport above,* and at such a level a second liquid or rigid boundary could again be introduced which would be both dynamically stable and horizontal, without any expansion potentials in the layer immediately above. But the possibility of a dynamically stable horizontal lower boundary for a system of two liquids, only, is predicated upon an expansion of the upper homogeneous layer.

It is of interest to note that *when the liquid boundary thus occupies a vertical position with reference to the trajectories of accelerated flow which causes it to become depressed, this implies that the average velocity of the entire upper homogeneous layer has actually become reduced by acceleration from above,* since the depth (thickness) of the layer after (*during*) acceleration (H_1) is now greater than its thickness before (D_1) and its

average velocity must therefore have been reduced in proportion to this increase in its thickness. Our conclusion, however, still rests upon the assumption that an actual increase in velocities must have occurred in the upper portions of the homogeneous layer, only to be outweighed in the average by retardations in its lower part, since this

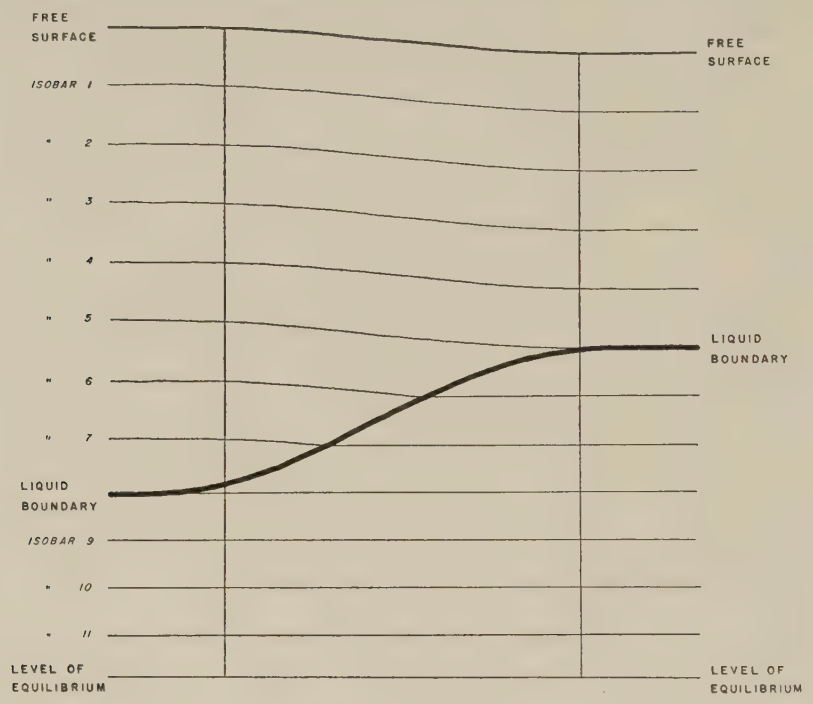

Figure 5. See text.

assumption is a necessary basis for the development of all the conclusions here advanced.

3. If instead of introducing our liquid boundary at the depth (D) of the rigid bottom assumed under point *1* we retain the rigid bottom and introduce a liquid boundary at some level above, letting the general conditions of flow remain unchanged (fig. 6A) we will get an entirely different result from that arrived at under point *2*, above.

It is evident that instead of becoming depressed by acceleration the liquid boundary must now rise according to the trajectories similar to (but not identical with) those shown in Figure 4A. This means that

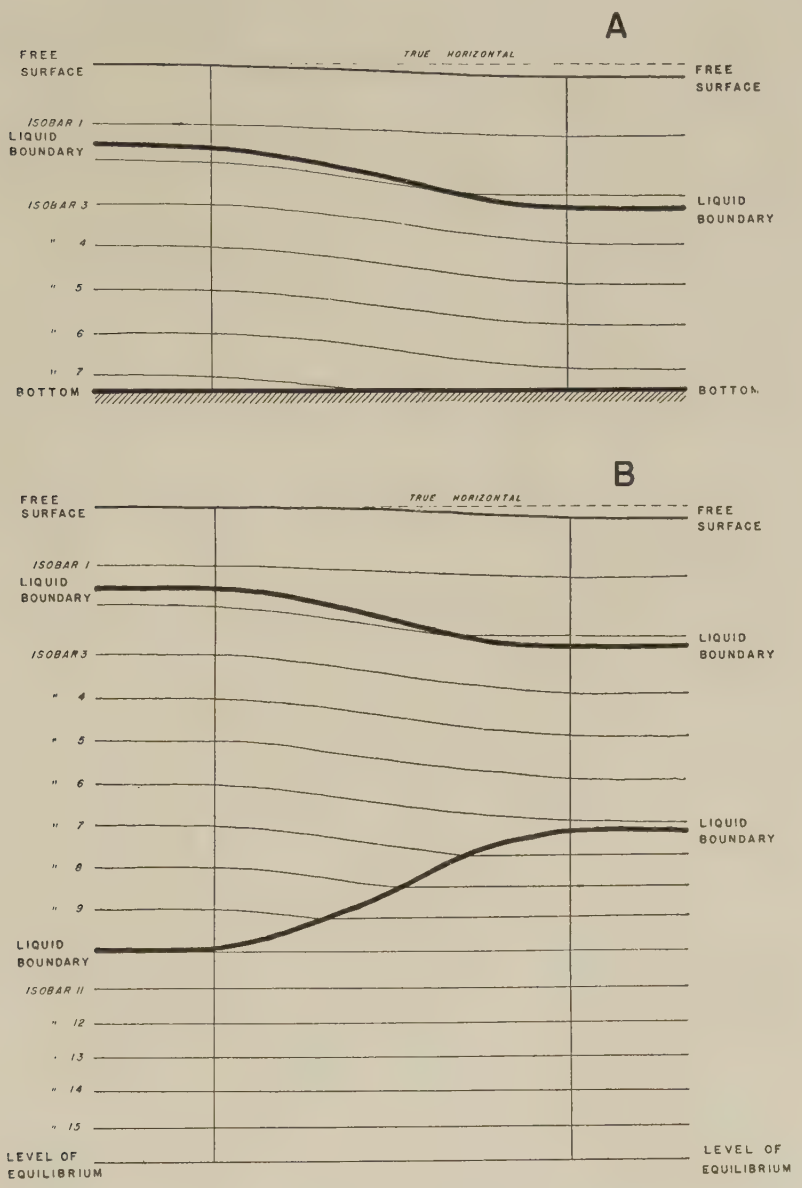

Figure 6. See text.

heavier water will reach to higher levels downstream instead of upstream, which must add a dynamic gradient in the upstream direction due to the distribution of mass to the upstream gradient already established by the surface depression.* The compensation acceleration will no longer be uniform from surface to bottom but must increase between the highest and deepest levels of the liquid boundary, becoming constant again at higher values below. Under these circumstances the resultant retardation maximum at the bottom and the suppressed tendency for the bottom layer to expand must be even more accentuated than in the presence of only one single homogeneous layer, as assumed under point *1*. Therefore if, as under point *2*:

4. We again introduce a *second* liquid boundary layer at the level of the rigid bottom assumed under points *1* and *3*, this second liquid boundary must now become depressed by acceleration in the downstream direction (fig. 6B); and a dynamically-stable horizontal isobaric surface may now again develop at a still deeper level in the manner already discussed under point *2*. If the homogeneous surface layer contracts by acceleration as here assumed, it should be noticed that it requires at least 2 (not only one as by expansion of the surface layer assumed under point *2*) more layers of increasing density above the lower boundary of the system, to enable this boundary to become horizontal and stable. Since, however, we are always dealing not only with three but with numerous layers in any ocean current, this limitation need not concern us here. What interests us at this point are the special conditions under which the various liquid boundaries in a system of multiple stratification may ascend or descend downstream by acceleration from above.

5. It will be noticed both under point *2* and point *4*, and can easily be reasoned out for all conditions of multiple stratification, that *the lowest intermediate liquid boundary above a horizontal isobaric level defining the lower limit of any given current system, must always descend by acceleration from above.* Applying the continuity principle again this means that *acceleration from above must cause an increase in the velocities in the lowermost as well as the uppermost part of the current system*, and a reduction of velocities in the intermediate portions under all conditions of multiple stratification. In a current consisting of two layers or more, the particular velocity curves before and after

* Which will undoubtedly be reduced accordingly to maintain a balancing compensation mass transport.

acceleration must therefore have at least two intercepts, as shown in Figure 7, not only one as in the case of an homogeneous liquid moving over a horizontal rigid bottom as discussed under point *1* (fig. 4B) while the cumulative mass transport curves must have at least one intercept between top and bottom instead of none (comp. fig. 4D).

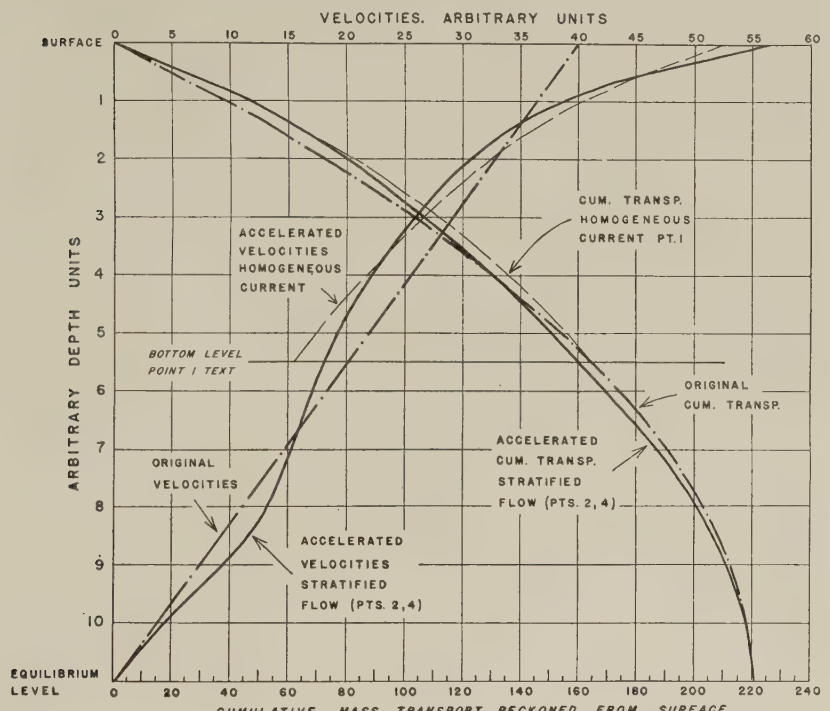

Figure 7. See text.

It is evident that if lateral expansion is excluded, mean trajectories in vertical perspective must follow the lines of equal cumulative mass transport reckoned from zero at the top or at the bottom of the system. The level of the intermediate intercept of the cumulative mass transport curves therefore becomes of very great importance by defining the depth above which the trajectories must ascend and below which they must descend by acceleration from above.

If this intercept is located above the lower boundary of the homogeneous surface layer, even the homogeneous layer itself must expand

(see point 2), and this would seem to be the case in the longitudinal profile of the Caribbean Current shown in Figure 3, which shows a slight downstream descent from about 70 to about 125–150 meters depth even of the upper isohaline for $36.5^0/_{00}$, which would place the intercept somewhere around 50 meters depth perhaps, and this may not at all be an unreasonable assumption. The picture further shows a thickening of the layers (isohaline intervals) down to the $35.0^0/_{00}$ isohaline, indicating this to be the range of intermediate retardation. Below the $35.0^0/_{00}$ isohaline we then again have the lower acceleration.

While the Caribbean Current is thus offered as an illustration of the general principles brought out in the preceding, on the assumption that they do play an important role in producing the results observed, the author is of course fully aware that lateral expansion, directly induced changes in the surface layer; and mixing processes and friction which we have here completely disregarded, also enter importantly into the determination of actual conditions in this as well as in all other ocean currents. Due to the topographic limitations of the region and the absence of other current systems on a corresponding order of magnitude, the Caribbean Current does, however, offer a closer approximation to a one-way flow through a rigid channel than most current systems in open oceans. It therefore seems reasonable to assume that *the general dynamic ascent of the current must in a considerable measure be due to direct acceleration by the trade-winds* operating over a finite bottom of insufficient depth and heterogenity of the deeper layers to permit the establishment of a lower horizontal isobaric surface in relation to which the calculated surface ascent would disappear. It thus seems indicated that the calculated ascent actually observed offers direct evidence of acceleration of the Caribbean Current by the trade-winds.

Having thus found a possible explanation for the general longitudinal slope of the Caribbean Current, we may now turn our attention to the conspicuous deviations from this general trend occurring around the Honduras-Jamaica ridge, where the water-masses rise and descend in conformity with the bottom topography, and where we consequently find a depression in relative dynamic topography above the surface. Similar relations between longitudinal hydrographic profiles and bottom topography have already been discussed by Defant and others (see Defant, 1929, pp. 46–54) in terms of internal waves and of the influence of bottom topography upon the vertical

lines of flow, without discussion of the secondary effect upon the relationship between calculated dynamic topography and horizontal direction of flow, although the effect upon horizontal lines of flow taken separately have been discussed quite extensively by Ekman (see Ekman 1928). In the writer's opinion, however, Rossby's revival of Bernoulli's theorem (Rossby, 1936) in oceanographic thought introduces a much more promising line of approach for the discussion of this and similar phenomena in the sea.

According to Bernoulli's theorem, a constriction in the channel of flow must cause an increase in longitudinal velocity accompanied by a reduction in pressure. Since the surface of the ocean may be considered level and horizontal with reference to the area of the current cross-section, and since furthermore a current in a stratified liquid will to a great extent move the various strata as though they were in separate cells (see Rossby, 1936) we may regard a rise of the bottom as for instance towards the Honduras-Jamaica ridge as a factor inducing acceleration from below. On the continuity principle, this must result in a thinning out of all the lower layers in proportion to how they are affected by the acceleration from below. If the acceleration extends to a certain level B, this means that the height of all layers below this level must be reduced and the lower layers in consequence displaced upwards above their normal level in open waters as they pass over the bottom elevation. If our assumption of an accelerating effect of the bottom elevation according to Bernoulli's theorem is correct, it *a priori* excludes the other possibility that the reduction in the height of the lower layers should lead to a descent of their upper boundaries towards the bottom, since this would require a great and unexplained retardation of the uppermost layers (above the level to which the acceleration from the bottom extends) to allow a compensating vertical expansion, as well as a complete retardation of all layers below the threshold as their normal levels successively impinge upon the ascending bottom.* This, in other words, would identify the accelerating effect of the vertical constriction only with

* That the uplift could not extend from threshold level to infinite depth, and that some of the lower layers in the deeper basins will therefore actually be completely stopped after some slight ascent, goes without saying. What we are here considering and attempting to rule out is merely the possibility that no uplift at all might occur even in the relatively faster moving layers advancing toward the ridge at the upper levels below the threshold depth.

the abstract mathematical summit of the ridge, but not with its ascending slope, which would be an illogical assumption in itself. These vertical oscillations of the lower layers in conformity with the bottom have also, as above mentioned, already been subjected to mathematical analysis by Defant and others on the simplifying assumption that the variations in bottom elevation follow a wave-like pattern, and we are indebted to these investigators (Defant, 1929, pp. 46–54) for the development of suitable equations for the calculation of the vertical distribution of this bottom influence under ideal abstract conditions. These equations also demonstrate the fact that the reversal of phase (descent with ascending bottom) may theoretically be expected to occur under various circumstances in the uppermost layer nearest to the free surface (Defant, 1929, pp. 47–48). This is also quite in accordance with our observations of the Caribbean Current as it passes the Jamaica-Honduras ridge (see fig. 3). Möller and Merz (1928) have finally reported observations from the Bosporus which form a very interesting parallel to the conditions observed in the Caribbean Current in that they give an excellent demonstration of the conformity between isopycnal surfaces and the bottom profile. A comparison between the Bosporus and the Caribbean profiles is the more interesting because there is in the former case a well-defined current and counter current superimposed upon each other in the same vertical, while the situation in the passage of the Caribbean Current over the Jamaica-Honduras ridge is simpler because of the absolute predominance of a single direction of flow from surface to bottom in the path of the main current over the highest threshold, with only comparatively insignificant and mainly or entirely *laterally* adjacent counter-current movements. On the basis of this general agreement between theoretical considerations and field observations, we may therefore safely assume as an established fact that acceleration from below caused by a rise of the bottom must result in an uplift of the lower layers involved in the motion. This rise of the lower and accordingly heavier layers must further result in the reduction of the relative dynamic elevation of the the surface, thereby releasing potential energy for a secondary acceleration to start from above. Since this reasoning is equally applicable regardless of whether the accelerating factor is of a static character in bottom topography or of a dynamic nature in the lower boundary surface of the current, it may be stated as a general principle that in a liquid stratified in point of density an acceleration starting

from the lower boundary of flow must result in a loss of dynamic height at the upper boundary and proportionately at all intermediate isobaric surfaces and must therefore induce a secondary acceleration from above. As we have already seen (page 11), this acceleration from above should, if it develops freely, tend to produce a downward deflection of the deeper intermediate layers, and this downward deflection might now be expected to establish an equilibrium at some intermediate level with the uplifting tendency of the acceleration from below. In the case of the Caribbean Current crossing the Jamica-Honduras ridge, this downward deflection from above is very evident in the courses of the 25° isotherm and the $36.5^0/_{00}$ isohaline (see fig. 2), and the equilibrium level would seem to be situated at about 200 meters depth.

Conversely, the descending slope on the downstream side of a ridge must cause a retardation starting from the bottom, with consequent expansion and descent of the lower and heavier layers. This again gives rise to an increase in relative dynamic elevation of the surface which causes a secondary retardation to begin from above, and it thereby serves to reconvert the potential energy previously converted into kinetic energy for the passage of the shallow ridge into potential energy again. In this we have an illustration of the *regulatory function of the potential energy content of the longitudinal dynamic gradient.* The principle that the retardation from below must induce a secondary retardation from above in the stratified current is also of general validity regardless of whether we are dealing with solid bottom or an internal boundary sheet. When retardation or acceleration starts from below, the relationship of dynamic contour lines to lines of flow will be the reverse of that obtaining when the influences originate from above, since we have seen that *acceleration from below must cause a descent of calculated dynamic slope throughout the layers involved, a retardation, on the other hand, being accompanied by an ascent.*

By the reasoning here set forth, the author makes no claims beyond that of having offered for consideration what appears to him to be one possible set of explanations both for the general trend of longitudinal dynamic slopes in the Caribbean Current and for the conspicuous undulating deviation from this general trend occurring over the Honduras-Jamaica ridge as shown in Figure 3, in the hope that whether accepted or refuted these suggestions may at least contribute to the final solution of the problems involved if only as an introductory basis for the discussion of a concrete case.

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Contribution No. 150

THE SIGNIFICANCE OF THE MISSISSIPPI RIVER DRAINAGE FOR BIOLOGICAL CONDITIONS IN THE NORTHERN GULF OF MEXICO

By

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Plankton collections and bottom hauls made during the 1935 expedition of the "Atlantis" to the Gulf of Mexico suggested that there is a zone of high productivity in the shallow water area near the mouth of the Mississippi, and since the effect of river outflow on ocean life is a phase of marine biology which has not yet received adequate attention, further investigation seemed desirable.

Atkins (1926) published tables of the phosphate distribution in the vicinity of Plymouth Sound which show that in that region the rivers contribute little phosphate to the ocean, and in the same year Harvey obtained similar results for nitrate. But Atkins had pointed out before (1923) that in certain regions the incoming nutrients may be highly significant. His conclusion was based largely on the data of McHargue and Peter (1921) who estimated that in the Mississippi River the amount of soluble phosphorus liberated each year is about 62,188 tons, and, in addition, the suspended matter, which averages 7469 million cubic feet per annum, contains .15% P in combined form.

Harvey (1928) again pointed out that in the rivers of the Plymouth Sound region the nutrients are largely exhausted by plant growth in the tidal or even the non-tidal zone, but he suggested that it was probably not the case in a large river such as the Amazon. Hesse, Allee, and Schmidt (1937) concluded that coastal effluents are quite important and even suggested that they are in part responsible for the fact that the Atlantic, which receives a large proportion of the earth's drainage, has a higher nutrient content than the Pacific.

The present work was therefore undertaken during the 1937 cruise of the "Atlantis," jointly sponsored by the Woods Hole Oceanographic Institute and Yale University (Bingham Oceanographic Laboratory), in an attempt to determine whether or not the incoming nutrients from the Mississippi have an observable quantitative effect on plant growth and nutrient matter present in the Gulf of Mexico.

I want to express my gratitude to A. E. Parr for giving me the opportunity to work on this problem and for his many valuable suggestions. I am also indebted to A. A. Hirsch of the New Orleans Sewerage and Water Board Company for much information and advice about the Mississippi River.

* Joint Contribution from Woods Hole Oceanographic Institution (No. 150) and Bingham Oceanographic Foundation.

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METHODS

The water samples were collected with Nansen bottles in the usual way, except stations B to H, which were surface samples drawn with a bucket thrown from the rail of the ship. Preparation of plankton collections and analyses of chlorophyll, soluble P, and soluble copper were done immediately; plankton weights and the remainder of the chemical analyses were obtained later from preserved samples. The positions of the stations where data of this sort were collected are shown in figure 19.

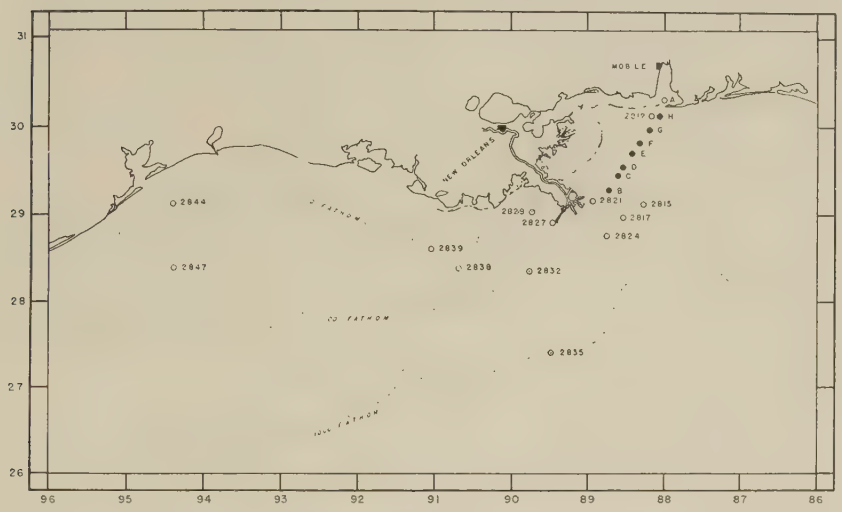

Figure 19. Position of stations referred to in this article.

Phosphate analyses were made according to the procedure described by Atkins (1923).

The copper test is a colorimetric determination described by Callan and Henderson (1929). A solution of sodium diethyl-dithiocarbamate is added to the sample to be tested. The copper salt of this substance is extracted with amyl alcohol, as suggested by McFarlane (1933), and for the colorimetric comparison I use a .001 N solution of potassium dichromate, which has the same color, the depth of which varies in a linear manner with that of the copper solution. When 50 ml. of water are used for the test plus .5 ml. of the reagent and 4.97 ml. of amyl alcohol, the .001 N. $K_2Cr_2O_7$ is the colorimetric equivalent of a copper concentration in the sample of .030 mg. per liter. The procedure of Haddock and Evers (1932) for the removal of iron is optional. Iron contamination is readily detected because it has a slightly reddish tint. It is unstable in amyl alcohol, fading after four or

five hours, whereas the copper color persists several days, so that it is possible to determine the copper content after the iron contamination has disappeared.

The chlorophyll was determined by a modification of Harvey's method (1934). The phytoplankton was removed from a liter or more of water by means of a quantitative filter paper and after separation of the chlorophyll in saponified form (Riley, 1937), it was measured colorimetrically against the Harvey standard.

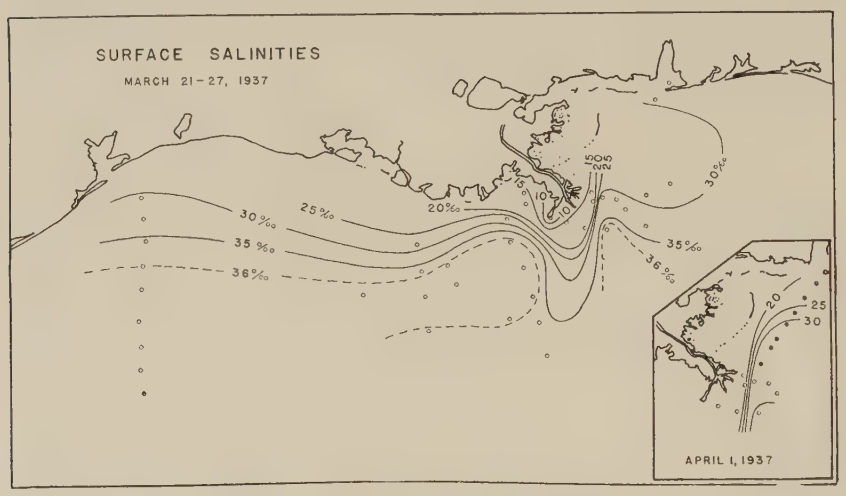

Figure 20. Distribution of surface salinities.

Plankton collections were made for the purpose of determining the weight of organic matter, and in some cases for copper and phosphate tests. One or two liters of water were filtered through a thirty-five second membrane filter, which removes all particulate matter of a diameter greater than .6 micron. The material was scraped from the filter after having been washed with distilled water to remove as much of the salt as possible, and was preserved with formalin. It was afterwards washed again, dried for two two days at 60° C., weighed, ignited, and weighed again, the difference being approximately the weight of organic matter in the sample. Copper tests were made on the ash. In the cases where phosphate tests were made, it was necessary to oxidize the whole sample, since ashing destroys part of the phosphate.

PHOSPHATES

The values obtained for soluble phosphorus in the surface waters varied from 2 to 16 mg. per m^3. The latter values were obtained at the mouth of

the Mississippi near Southwest Pass and Pass à Loutre, and the next highest figure, 11 mg. per m^3., was in Mobile Bay. In the Gulf itself, the analyses ranged from 2 to 8 mg., with an average of 3.8. Figure 21 shows the general distribution of phosphates in the surface layer. The higher values are found around the mouth of the Mississippi and extending eastward toward Mobile Bay and westward to about longitude 91°.

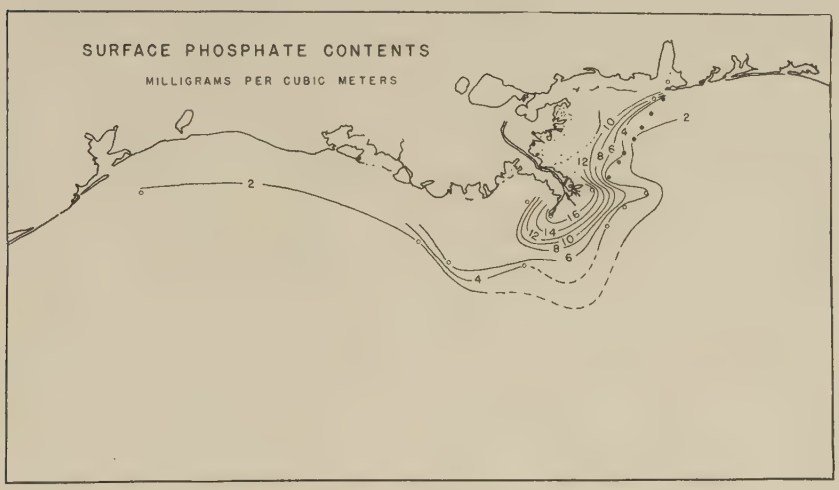

Figure 21. Phosphate distribution in surface layer.

This zone of high phosphate concentration is quite superficial. There are five stations within the zone where analyses were made at depths ranging from 10 to 25 meters. At those depths the mean amount of soluble P was 3.6 mg. per m^3. as compared with 5.8 at the surface at the same stations. A similar result was obtained at Pass à Loutre, where the phosphate was 16 mg. at the surface and 11 mg. at 13 m. In Mobile Bay, on the other hand, it was 11 mg. at the surface and 15 at 6 m. Outside the zone of high surface phosphates there are only two stations available for study of vertical distribution, and their results are contradictory, so that no generalizations can be made.

PLANKTON MEASUREMENTS

The chlorophyll data are expressed in the arbitrary Harvey units, of which one unit corresponds to about .88 gamma of chlorophyll. It is impossible to convert these figures into absolute weights of phytoplankton, but the chlorophyll analysis serves as an index of potential photo-synthetic activity. As such, it is more useful in studies of productivity than plankton

weights, which are of course measurements of animals, bacteria, and detritus, as well as phytoplankton.

The mean amount of chlorophyll in all analyses of Gulf water was 6.7 Harvey units per liter. In this case also, it is possible to draw a rough zonation around the mouth of the Mississsippi. The region where the chlorophyll is highest, above 8 units per liter, extends westward from Mobile Bay to some undetermined point beyond station 2839. If it goes as far as Galveston, it is reduced to a narrow strip near the shore. The areas containing 6 to 8 Harvey units per liter form thin bands around the eight

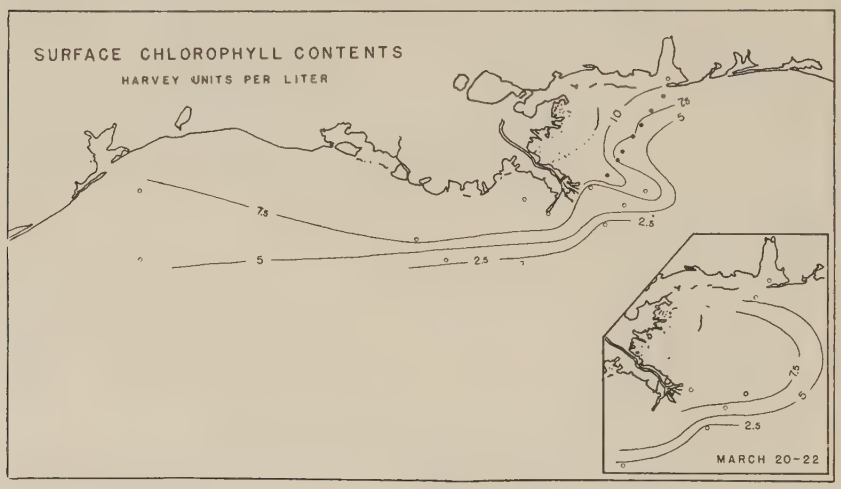

Figure 22. Chlorophyll distribution in surface layer.

unit line and extend westward past its observed limits. There remain four stations on the east and south, where the range of chlorophyll was from 1.6 to 5.9.

Station 2812 does not fit in with the remainder of the analyses. A surface value of 3.6 Harvey units per liter was obtained there, whereas in the waters immediately around it on the east, north, and south, the chlorophyll measured eight or more units. This, however, can be ignored because of evidence based on salinity distribution. According to Dr. Parr, the surface salinities show two distinct situations, observations during the early part of the cruise giving a consistent picture, which, however, cannot be combined with observations made on the return trip between the Mississippi and Mobile (see fig. 20). Heavy weather intervening between these two parts of the cruise probably caused the change. Since most of the special observations in this area were made on the return trip, most of the data on chloro-

phyll, phosphate, and copper distributions between Mobile and the mouth of the Mississippi river correspond to the salinity distribution of April 1. Only in the case of chlorophyll does it seem necessary to give two separate interpretations.

The only sample of completely fresh water, which was taken at New Orleans, had a value of 12.8 units per liter. This was slightly higher than any of the analyses made in the Gulf but was by no means large by comparison with the usual values obtained in fresh water. It is obvious that the turbidity of the Mississippi is a strong inhibiting factor on the growth of phytoplankton, which would otherwise be very great because of the large quantities of available nutrients. The five analyses near the mouth of the Mississippi and in Mobile Bay ranged from 4.8 to 11.1. Here also, turbidity was an important conditioning factor, and, in addition, the salinities were probably unfavorable.

The results obtained from the plankton weights closely parallel the chlorophyll measurements. The dry weights of organic matter per liter of water varied from 1.0 to 20.6 mg. in Mobile Bay and near the mouth of the Mississippi. In the Gulf the range was from .2 to .5 at the surface, the lowest values of .2 and .3 mg. being at stations 2832 and 2838, where the chlorophyll was also very low.

The very high ratios of organic matter to chlorophyll which occur near the river indicate large quantities of organic detritus. The ratios fall so rapidly as one proceeds out into the Gulf that it seems likely that practically all the organic detritus of fresh water origin is removed from the surface water before it gets more than ten or fifteen miles from the mouth of the river.

The plankton was not identified carefully, but superficial examination indicated that the flora is fairly constant qualitatively throughout the entire area studied in spite of the wide range of salinities. No freshwater phytoplankton was noted in the water at station 2827, which had a salinity of only 5.95‰.

COPPER

The work on copper was undertaken because it was thought that it might supply evidence on the nutrient conditions in the Gulf. In an as yet unpublished investigation of the copper cycle in fresh water it was shown that copper is readily absorbed on organic detritus, and the amount so combined is frequently much greater than that occurring in the living organisms of the plankton. It can therefore be used as an approximate index of the amount of detritus in a given sample of seston.* But since it

* A general term, borrowed from freshwater ecology, for the combination of plankton and detritus which is removed from the water by the usual filtration and centrifuge methods.

is apparent that freshwater detritus is not a very important source of nutrients in Gulf waters, the work on copper is not significant from that standpoint.

There are, however, certain aspects of the copper problem that are in themselves worthy of brief mention. The presence of copper in sea water has been detected by Dieulafait, Rose and Bodansky, Prytherch, and others. Prytherch found that the quantity in the sea is very much less than that in fresh water and suggested that inorganic precipitation takes place. The horizontal distribution of copper in the Gulf, shown in figure 23, confirms

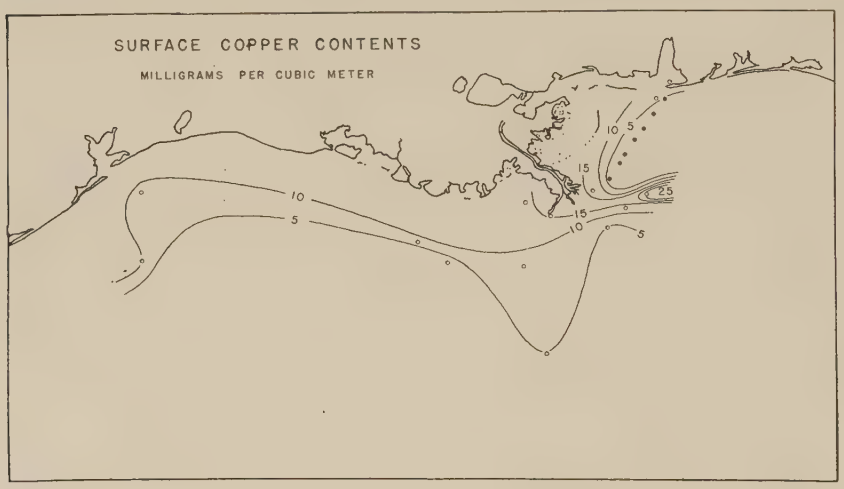

Figure 23. Distribution of copper in surface layer.

his results in so far as the amount near the Mississippi is large, and it decreases progressively with increasing salinity.

The total range of soluble copper in all analyses was 1 to 25 mg. per m^3. The very high values of 20–25 mg. obtained at station 2815 do not fit with the rest of the picture. It is not possible to say definitely whether or not there was an error in these analyses, but too much significance should not be attached to a single set of isolated values. Except for this station, the range of copper was from 1 to 15 mg., with the highest values in water of low salinity. Furthermore, analyses of the vertical distribution of soluble copper near the mouth of the river show that the amount is greater in the low salinity surface layer than at the lower levels where the salinity is higher. But none of the analyses obtained in the Gulf were negative, indicating that removal by precipitation, if it occurs at all, is not complete. It thus seems probable that copper is not a limiting factor in the open ocean to those animals which require it for the synthesis of hemocyanin.

At station 2835 tests were made to determine the vertical distribution of soluble copper. A slight accumulation was noted in the hypothalassa (fig. 24), which was much less than that recorded for such substances as phosphate and nitrate, which are biologically more active. The data on

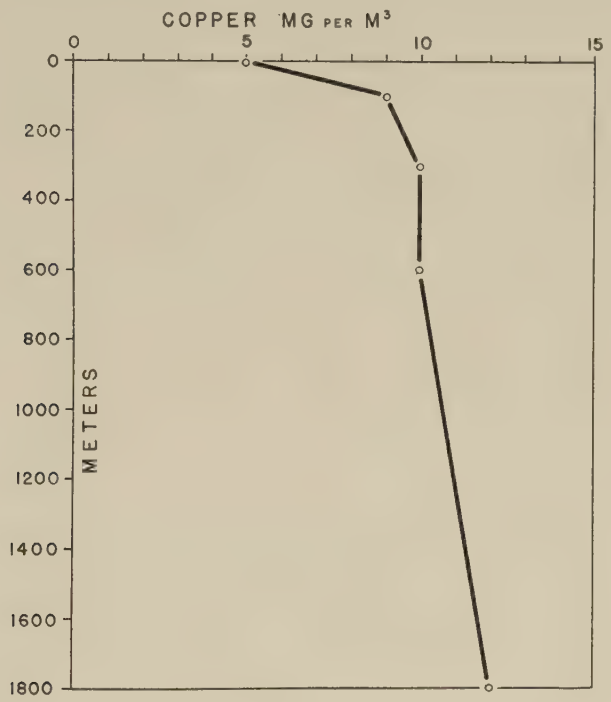

Figure 24. Vertical distribution of copper at station 2835.

vertical distribution and seston copper both resemble conditions found in freshwater lakes and indicate that the distribution factors are similar, with the emphasis placed on adsorption equilibria between soluble and seston copper, rather than on inorganic precipitation.

DISCUSSION

The nutrient content of the Mississippi River

Analyses of soluble phosphorus at stations 2821 and 2827 near the mouth of the river where mixing with sea water was slight gave values of 16 mg. per m^3. at the surface. At the former station 11 mg. were found at a depth of 13 m. One analysis was made of soluble P in the river proper, where a

value of 6 mg. per m^3. was obtained at Carrollton, just above New Orleans, on April 5. This difference cannot reasonably be accounted for on the basis of regeneration of combined phosphorus or discharge from the New Orleans sewerage disposal plant. The former is probably not more than 2 mg. per m^3.; the latter, according to an estimate by Mr. Hirsch based on the normal amount of phosphorus in human excreta and on the amount of phosphate washing powders used in New Orleans, is about 1500 kilos per day, which at the rate of flow at that time would average only .6 mg. per m^3. The difference is probably not important, for, as Mr. Hirsch pointed out, the nitrate content of the water above New Orleans varies irregularly, and it is quite possible that phosphate behaves in a similar manner.

The amount of phosphorus in combined form appears to be less than half as much as values obtained for soluble P at the mouth of the river. Analyses of sediments taken from the river at Carrollton are shown in the table below:

	Mg. of P/g. of mud
June 20–July 11, 1936	.011
October 10–30, 1936	.004
Dec. 12, 1936–Jan. 9, 1937	.053
January 9–31, 1937	.0008
Jan. 31–Feb. 6, 1937	.010
Feb. 6–Mar. 13, 1937	.006
Mar. 13–27, 1937	.007
Mar. 27–May 1, 1937	.004

These sediments are Berkefeld residues of weekly composite water samples collected twice daily and thus represent a mass average for a given period. The average of all samples is .012 mg. of P per gram of mud, and since the amount of sediment is usually less than a gram per liter (the most recent average that I have is .65 g./1. in 1935), it appears that the amount of combined phosphorus is rather small. At station 2827 it was .005 mg. per gram of mud, which was .002 mg. less than the amount at New Orleans during the same period. The weight of sediment collected at that station was 294 mg. per liter, so that the amount of combined P was .0016 mg. per liter, only one-tenth the value of the soluble P.

The discharge of the river at that time was 34,000 m^3. per second. If the data obtained at station 2827 may be regarded as accurate enough to be used as an estimate, the Gulf was at that time receiving 47,000 kilos of phosphate in soluble form per day, and an additional 4,700 kilos of combined P.* The latter figure is probably too low, for some of the mud had already become sedimented, but the value would almost certainly not be more than 25,000.

* E. g. enough to contribute one mg. per m^3. daily to 1000 square kilometers of surface layer, 50 meters deep.

It is obvious that these values represent only rough approximations. The averages obtained by McHargue and Peter in 1921 for soluble phosphorus are about three times as high, which is not an unreasonable difference, since both the seasonal and the annual variations might well be large. It is more difficult to explain the great discrepancy in the data for combined P, since their values are over one hundred times as great as mine. But regardless of which estimate is more nearly correct, it does not alter the general conclusion that the situation is a different one from that described by Atkins in the Plymouth Sound region. The phosphates in the Mississippi are not exhausted before they reach the mouth of the river but are poured into the Gulf in large quantities, in a form readily utilized by marine phytoplankton.

The same is probably true of nitrogen compounds. No analyses are available either of Gulf waters or at the mouth of the river, but analyses at New Orleans indicate that the quantities are rather large. I am indebted to Mr. Hirsch for the following data, which are approximate averages for 1935:

Ammonia N	20 mg. per m^3.
Albuminoid N	350 mg. per m^3.
Nitrite N	5 mg. per m^3.
Nitrate N	200 mg. per m^3.

The average nitrate concentration in the river is thus approximately the same as the accumulated nitrate concentration in the depths of the ocean but much greater than the normal concentration in the marine surface layers into which the river outflow mixes itself. The ammonia and albuminoid nitrogen contents of the river (assuming that the latter is decomposed sooner or later with the liberation of NH_3) are also many times as great as those normal to the marine surface layer.

The effect of the Mississippi on the Gulf

It has been shown that the Mississippi releases a large quantity of phosphate into the Gulf. From two-thirds to nine-tenths of it is in soluble form, capable of being utilized by marine plants as soon as the river water becomes mixed with Gulf water. The amount of soluble phosphate per unit volume in the river is approximately four times the mean amount found in the sea water of the surrounding region. It might therefore be expected to exert a considerable biological influence provided the amount of flow from the river is great enough to cause a significant increase in the phosphate content of the surrounding waters.* That such an increase does take place is indicated by fig. 21.

It is assumed that this increase is due largely to mixing with the river water because: 1. The low salinity of this water proves that such mixing

* See footnote on p. 68.

has occurred. 2. There is little evidence of an important increase by other means, such as regeneration from the mud by vertical mixing or upwelling of deep water. The greatest concentration of phosphates is found in the low salinity surface layer, with lesser concentrations at depths of ten to twenty-five meters. But regeneration from the bottom would suggest a greater concentration at the lower levels, and the presence of a distinct salinity gradient is ample evidence that vertical convection had not occurred to any great extent.

In the same general region phytoplankton production appears to be high. As may be seen by comparison of figures 21 and 22, the area of high chlorophyll content coincides with that of high phosphorus except that the former extends somewhat farther west and not so far south.

It is obvious that the amount of chlorophyll per unit volume is greater in the waters near the Mississippi. It appears also that the absolute amount is greater. This may be demonstrated in the following way: Station 2829 was chosen as a typical example for the region of high chlorophyll content, and the most useful one available because of the completeness of its data. A graph was drawn of the chlorophyll distribution down to 35 m., which was probably about the compensation point, since the chlorophyll was fairly low in spite of a high phosphate content. The curve was integrated planimetrically, and it was found that a column of water extending to a depth of 35 m. and 1 cm.^{2} in cross section would contain 23.2 Harvey units of chlorophyll. Farther out in the Gulf, at station 2838, the chlorophyll measured 2.6 units at the surface and 1.8 at 20 m. At this station the amount of chlorophyll per cm.^{2} in the first 20 m. was 4.4 units. If we assume that the water contained a uniform concentration of 1.8 units from 20 m. down to an indefinite depth, then the compensation point would have to be at a depth of 120 m. in order to make the photosynthetically active chlorophyll content as great as at station 2829. At 2824, a similar deep water station, it would have to be at 135 m. These values are impossibly deep, and we may conclude that the absolute amount of chlorophyll is greater in the region around the mouth of the Mississippi except in the very shallow water near shore.

A higher standing crop of phytoplankton in the Mississippi region means that the productivity of that area is greater provided there are no significant differences in the rates of phytoplankton growth and of consumption by zooplankton. There is a more plentiful supply of nutrients near the river to balance against the slightly higher temperature of the offshore waters. The rate of consumption appears to be more important from the standpoint of productivity than the growth rate, and such evidence as is available (ratios of total organic matter in the plankton to chlorophyll and the indirect evidence of the distribution of larger animals in the Gulf) indicates a larger quantity of zooplankton near the Mississippi. It may therefore be

concluded tentatively that the productivity is greatest in the high chlorophyll zone, although the matter cannot be settled definitely until more adequate data are available on the rate of plankton turnover in the Gulf.

Since the assumption is warranted that an increase of phosphorus content leads to greater phytoplankton productivity provided its growth is not limited or conditioned by other factors, the conclusion is permissible that the zone of high phosphate, and consequently the Mississippi itself, is an important factor in the productive area around the mouth of the river.

It was pointed out above that the zones of high phosphorus and high chlorophyll do not exactly coincide. The area where there is a high direct relationship lies within a radius of thirty or forty miles from the mouth of the river except toward the west, where it extends about eighty miles. Outside this region the relationship is slight, and consequently the correlation between phosphorus and chlorophyll in the entire area studied is low ($r = .10 \pm .05$). On purely theoretical grounds a low positive correlation or a correlation of zero is indicative of intrusion of phosphate into the area, since if the spring season begins with a more or less uniform concentration throughout the entire region, that part which has the greatest growth of phytoplankton will use the phosphorus most rapidly, thus leading to a negative relationship. This confirms the evidence presented above on the role of the Mississippi. But together with the fact that at none of the stations examined was there complete exhaustion of phosphate, it precludes the possibility that phosphorus is a limiting factor in these waters.

There are several possible explanations in regard to limiting factors:

1. Some other chemical substance or substances are involved.
2. The limiting factor is consumption by animals, which is rapid enough to keep the phytoplankton population below the level of complete utilization of phosphate.
3. During the spring season there are no limiting factors in the strict sense, but the greater quantity of nutrients near the mouth of the river conditions a higher plant growth there.

Figure 25 throws valuable light on the matter. Between salinities of 30.00 and 36.10°/₀₀ there is an inverse relation between salinity and chlorophyll with a coefficient of correlation of $-.68 \pm .16$. Below 30°/₀₀ the rate of increase of phytoplankton with decreasing salinity declines considerably. The data are too meagre for the remainder of the curve to be statistically significant, but there may be a secondary minimum at a salinity of about 10°/₀₀. The depression of phytoplankton growth in the lower salinities is partly due to turbidity. But the latter becomes apparent at the same point where the ratio of organic matter to chlorophyll begins to rise abruptly, that is, at a salinity of 18°/₀₀, whereas the depression of the chlorophyll curve is apparent at 30°/₀₀. Furthermore the inhibiting effect is not so marked in the Mississippi itself, where obviously the effect of turbidity is

greatest. Therefore, another factor is involved, probably salinity itself, which, in the brackish water zone, has an inhibiting effect on both marine and freshwater plankton.

The evidence just presented shows a definite relationship between chloro-

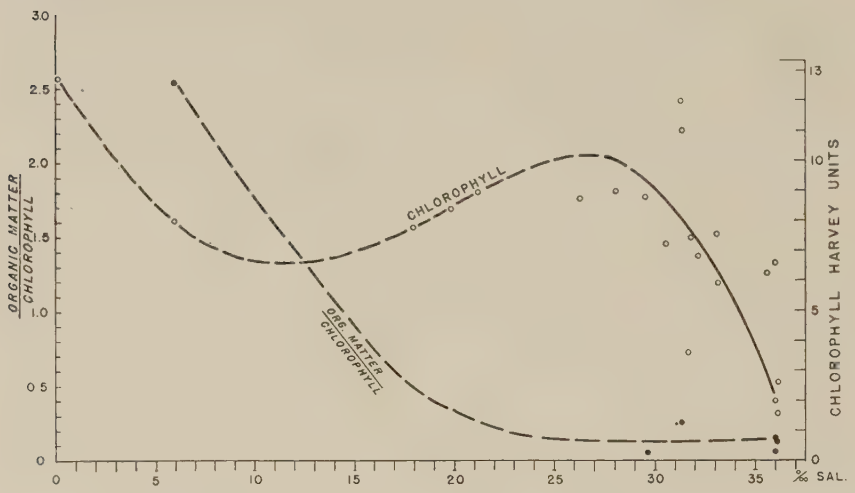

Figure 25. Relations of chlorophyll to organic matter and to salinities.

phyll and salinity. Up to a certain point, mixing of river water with the Gulf causes an increase in the phytoplankton crop. It is therefore probable that there is some nutrient salt in the river water, occurring there in higher concentration than in the Gulf and diffusing into it in much the same manner as phosphorus, which is a limiting factor in this region.

SUMMARY

1. The Mississippi River carries large quantities of nutrient salts into the Gulf of Mexico. The quantity of phosphate per unit volume is approximately four times as much as the amount found in the sea water of the surrounding region.

2. In the Gulf there is a superficial zone of high phosphorus content around the mouth of the Mississippi, extending from Mobile Bay westward to longitude 91°. Evidence is presented to show that this phosphorus is largely derived from the Mississippi and that the soluble phosphate of the river is more important in this respect than that in organic combination.

3. There is a zone of high phytoplankton content near the river which roughly coincides with the area of high phosphorus. A causal connection between the two is indicated.

4. It is suggested on purely theoretical grounds that some other nutrient which is discharged from the Mississippi in the same manner as phosphate is a limiting factor in this region.

5. A few notes are presented on the distribution of copper in the Gulf. It was present in all samples analyzed in both soluble and combined form. In deep water there appears to be a slight accumulation of soluble copper in the hypothalassa.

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TABLE OF OBSERVATIONS

*Station**	*Depth meters*	*Salinity* ‰	*Chlorophyll Harvey units per liter*	*Sol. Cu. mg. per m³*	*Sol. P. mg. per m³*	*Organic Matter mg. per liter*	*Seston Cu. mg. per m³*
A	1	31.47	11.1	9	11	2.9	3.2
	6	31.24	7.2	4	15	4.0	5.4
2812	1	31.70	3.6	9	8		2.3
	15	35.52	5.8	9	5		2.6
2815	1	29.62	8.8	25	4	.44	1.3
	25	36.08	5.0	20	4	.14	1.6
2817	1	31.56	6.2	11	3		
	25	36.17	2.5	8	2		
2821	1	18.01	7.8	12	16	4.27	6.8
	13	34.08	4.8	12	11	1.00	1.5
2824	1		2.0	5	4		
	25		1.7	8	3		
2827	1	5.95	8.1	15	16	20.60	7.2
2829	1	19.90	8.4	14	7	.49	.8
	10	26.40	10.2	7	2		
	20		4.8	7	2	.32	.3
	35		4.5	5	10	.81	.7
2832	1	36.05	1.6	7	4	.23	.5
2835	1	35.91		5			
	100	36.00		9			
	300			10			
	600			10			
	1800			12			
2838	1	36.10	2.6	3	6	.34	.4
	20	36.09	1.8	3	4		
2839	1	26.82	8.7	8	2		
	10	32.55	4.8	6	5		
2844	1	30.57	7.2	6	2		
2847	1	36.00	6.4	10	2	.38	.7
B	0	31.35	12.0	2	3		
C	0	31.85	7.4	4	3		
D	0	33.19	5.9	1	4		
E	0	33.17	7.5	2	2		
F	0	32.22	6.8	3	3		
G	0	28.03	9.0	2	2		
H	0	21.24	9.0	2	3		
Mississippi River New Orleans, La. April 5, 1937			12.8	15	6		

Seston Phosphorus
Station 2827. 1.6 mg./m³ at 1 meter; Station 2829. 0.5 mg./m³ at 10 meters; Station 2838. 0.3 mg./m³ at 20 meters.

* See figure, page 61.

(*Reprinted from* NATURE, *Vol.* 140, *page* 506, *September* 18, 1937.)

Consumption of Oxygen in Sea Water under Controlled Laboratory Conditions*

DURING a recent hydrographical cruise of the *Atlantis*, the oxygen consumption in samples of water taken from eighteen levels between surface and 4,600 metres depth at Station 2886 (32° 19′ N., 65° 59′ W.; June 19, 1937) was determined under controlled laboratory conditions. Two glass bottles (with ground-

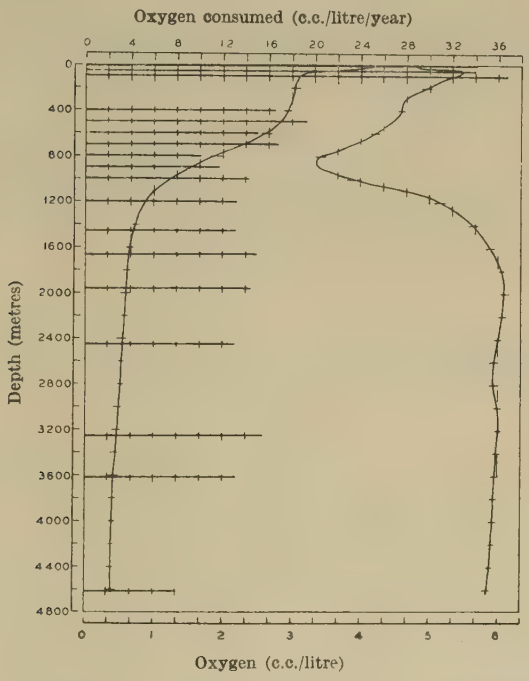

Fig. 1.

OXYGEN CONSUMPTION IN C.C. PER LITRE PER YEAR (OBTAINED BY MULTIPLYING MEAN DAILY VALUES BY 365) FOR VARIOUS DEPTHS SHOWN BY HORIZONTAL LINES REFERRED TO TOP SCALE; VERTICAL DISTRIBUTION OF OXYGEN, RIGHT CURVE REFERRED TO BOTTOM SCALE; VERTICAL DISTRIBUTION OF TEMPERATURE, LEFT CURVE, REFERRED TO TOP SCALE. DATA FROM *Atlantis* STATION 2886

glass stoppers) were filled from each of the Nansen water bottles as soon as they were brought on deck; one set of eighteen samples was stored at a temperature of 11° in an electric refrigerator and the other set

* Contribution No. 151 from the Woods Hole Oceanographic Institution.

at a temperature of 24° in the laboratory. After ten days of storage in darkness, oxygen contents of the two sets of samples were determined and subtractions of these values from initial oxygen contents of the samples gave results we have termed oxygen consumption.

The oxygen consumption at 24° ranged from 0·058 to 0·165 c.c. per litre per day, and at 11° it ranged 0·020 to 0·069 c.c. per litre per day ; higher values characterized water from levels below 1000 metres depth. The average oxygen consumption of all eighteen samples incubated at 24° was 0·1224 c.c. per litre per day, and for those at 11° it was 0·0487 c.c. per litre per day.

In an attempt to estimate what the oxygen consumption would have been if the samples of water had been incubated at their respective observed temperatures *in situ* (Fig. 1), it was assumed that the variation in oxygen consumption with temperature (between 25° and 2°) was of the form :

$$(1) \qquad \ln k = c - \frac{A}{T};$$

which equation after being differentiated and then integrated between the limits k_1, T_1, and k_2, T_2 results in a form of the Arrhenius equation :

$$(2) \qquad \ln \frac{k_1}{k_2} = \frac{Q}{R}\left(\frac{1}{T_2} - \frac{1}{T_1}\right),$$

which frequently represents in a satisfactory manner the effect of temperature on biological reactions over limited temperature ranges.

Upon determination of the constant Q (R is the gas constant) from the average consumption values at 24° and 11°, each of the 18 pairs of values obtained at these temperatures were reduced by means of the Arrhenius equation to values corresponding to observed temperatures (range 25°–2°) at the depths from which the samples were taken, and the means of each pair of values (after multiplying by 365) are plotted against depth in Fig. 1. It is realized that this method of extrapolation may not hold for this particular phenomenon over the entire temperature range of 25° to 2°, but it does furnish an approximation.

The results (Fig. 1) after reduction are too high, particularly in the deeper levels, to be used in estimating oxygen consumption *in situ* in the water column itself. For example, at Station 2886, water from the minimum oxygen layer (less than 60 per cent saturated, occurring approximately between depths of 700 and 1000 metres) had an average daily adjusted oxygen consumption of 0·0363 c.c. per litre, which is about 32 times greater than the value of 0·42 c.c.

per litre per year previously estimated for this layer; and water from between 1000 and 2000 metres had an adjusted daily consumption in the laboratory of 0·0385 c.c. per litre, which is more than 100 times greater than the more reasonable previously estimated value of 0·103 c.c. per litre per year for this part of the water column.

Thus, it appears that conditions in the sea, other than temperature, restrict the rate of oxygen consumption, and the above results are of interest since they indicate the potential rates of oxygen consumption throughout a water column of the sea when its equilibrium is disturbed by laboratory conditions.

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August 2.

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A Suggested Method for Representing Gradient Flow in Isentropic Surfaces*

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(*MS received July 24*)

EXTENSIVE USE is now being made of isentropic charts for the representation of flow patterns in atmospheric currents, and their use is being attempted in oceanography also. Their advantage lies in the property that any particle displaced adiabatically and maintained under hydrostatic equilibrium remains on its original surface. The purpose in using isentropic charts is, briefly, that they afford a means of determining the motion in a manner entirely independent of assumptions regarding the existence of gradient flow. At the same time it is desirable to know what the gradient flow would be, and a convenient method for determining it is needed.

The common methods of representing gradient flow, viz., by means of isobars or topography of isobaric surfaces, cannot be used for the sloping surface of an isentropic chart, and the following method is suggested to take their place.

Using right handed axes with the z-coordinate directed upward, the components of the gradient velocity (neglecting curvature of streamlines) are given by the equations of motion

$$v = \frac{a}{f}\frac{\partial p}{\partial x}$$

$$u = -\frac{a}{f}\frac{\partial p}{\partial y},$$

where f is the Coriolis parameter, and a is specific volume. Representing geopotential by Φ, the hydrostatic equation may be written

$$\frac{d\phi}{dz} = -a\frac{\partial p}{\partial z}$$

From this and the differential equation for an isobaric line in the x,z-plane follows an expression for the

*Contribution No. 153 from the Woods Hole Oceanographic Institution.

x-component of the horizontal pressure gradient:

$$\frac{\partial p}{\partial x} = \frac{1}{\alpha}\left(\frac{d\Phi}{dx}\right)_p$$

The subscript p indicates that the variation is taken along an isobaric surface (in the x,z-plane). Hence

$$v = \frac{1}{f}\left(\frac{d\Phi}{dx}\right)_p$$

with a similar expression for u. These are the equations which determine the gradient velocity from the topography of an isobaric surface.

Now consider any surface (such as an isentropic surface), which may be designated by A. For the variation of pressure in the x-direction along this surface one finds

$$\left(\frac{dp}{dx}\right)_A = \frac{\partial p}{\partial x} + \frac{\partial p}{\partial z}\left(\frac{dz}{dx}\right)_A.$$

Substitution in this of the hydrostatic equation and the expression for the horizontal pressure gradient gives an expression for $(d\Phi/dx)_p$, so that

$$v = \frac{1}{f}\left[\left(\frac{d\Phi}{dx}\right)_A + \alpha\left(\frac{dp}{dx}\right)_A\right]$$

with a similar expression for u. These permit calculation of the gradient flow in terms of the slope of the surface, the pressure gradient tangent to the surface, and the specific volume at the point in question.

When the surface A is assigned certain definite characteristics, the last equation may be simplified. For a level surface the first term on the right side drops out, for an isobaric surface the second term drops out, thus giving the two common expressions for gradient flow. Simplifications will be found also for isentropic surfaces in the atmosphere and in the ocean.

Meteorological Application

For an exact application of isentropic surfaces it is necessary that the fluid fulfil the two following conditions. The first of these is fulfilled by the atmosphere, namely, that two samples of air of the same specific volume mixed under constant pressure form a mixture with the original specific volume.

On the other hand, two samples of air having different moisture content but the same specific volume at a given pressure, do not have exactly the same specific volume when displaced adiabatically to another pressure. That this second condition is not exactly fulfilled is probably of no practical importance. It would seem sufficient to use a surface of constant potential temperature (θ) as the isentropic surface.

The last equation above, on substitution of θ for the subscript A, becomes the equation for the y-component of the gradient wind in a surface of constant potential temperature. Since α is the specific volume on a surface of constant potential temperature, it is given by the differential equation for an adiabatic process, namely

$$c_p\, dT - \alpha\, dp = dq = 0,$$

so that

$$\alpha\left(\frac{dp}{dx}\right)_\theta = c_p\left(\frac{dT}{dp}\right)_\theta\left(\frac{dp}{dx}\right)_\theta = c_p\left(\frac{dT}{dx}\right)_\theta.$$

Hence

$$v = \frac{1}{f}\left(\frac{d(\Phi + c_p T)}{dx}\right)_\theta$$

with a similar expression for u.

Here Φ and T are the dynamic height and temperature of the surface of constant potential temperature, and c_p is the specific heat of air under constant pressure. $(\Phi + c_p T)$ forms the stream function of the gradient wind in this surface. If isolines of this function are plotted on an isentropic chart, they form streamlines and serve the same purpose as isobars on a common weather map.

Oceanographic Application

Isentropic charts lose in distinctness somewhat when applied to the ocean. In the first place, two samples of water of the same specific volume at one pressure do not in general have the same specific volume at another pressure. As an example, consider two samples both of which have the specific volume .95970 ($\sigma_t = 28.00$) at the sea surface. One may have a temperature of 2° and a salinity of 35.00 ‰; when displaced adiabatically to a pressure of 3000 decibars, its temperature becomes 2.24° and specific volume .96000. Another may have a temperature of 3° and a salinity of 35.12; when displaced to 3000 decibars, its temperature becomes 3.26° and specific volume .96008.

In the second place, when two samples of the same specific volume but different temperature and salinity mix, the resulting mixture has a lesser specific volume than the original samples.

Probably these effects are negligible in most practical applications of isentropic charts. This remains to be definitely determined, as does the best practical procedure in locating the isentropic surface. The nicest procedure would be to determine the value of the specific volume that each sample would have if raised adiabatically to the sea surface, and define the isentropic surface as that surface having equal such values. Another method would be to use a true isosteric surface. A simpler, and probably sufficiently accurate, procedure is to use a surface of constant σ_t.

The exact surface chosen does not matter for the following development, so the symbol A will be retained. Designating standard by s and anomaly by a, in the usual oceanographic sense,

$$\Phi = \Phi_s + \Phi_a$$
$$\alpha = \alpha_s + \alpha_a,$$

so that

$$v = \frac{1}{f}\left[\left(\frac{d\Phi_s}{dx}\right)_A + \left(\frac{d\Phi_a}{dx}\right)_A + \alpha_s\left(\frac{dp}{dx}\right)_A + \alpha_a\left(\frac{dp}{dx}\right)_A\right].$$

It should be noted that the introduction of anomaly of geopotential involves the restriction that the level of zero geopotential must be an isobaric surface. Φ_s and α_s are functions of pressure alone and the first and third terms on the right cancel, so

$$v = \frac{1}{f}\left[\left(\frac{d\Phi_a}{dx}\right)_A + \alpha_a\left(\frac{dp}{dx}\right)_A\right]$$

with a similar expression for u. These may be used as they stand for computing the gradient current.

If, however, α_a may be considered constant along the isentropic surface, the determination of velocity is greatly simplified by writing

$$v = \frac{1}{f}\left(\frac{d(\Phi_a + \alpha_a p)}{dx}\right)_A$$

p is simply the pressure, and Φ_a and α_a the anomalies of dynamic height and specific volume, at the isentropic surface, so that $(\Phi_a + \alpha_a p)$ is easily computed for each station. This forms the stream function for the gradient current in the isentropic surface. When plotted on an isentropic chart it fulfils the same purpose as does topography for an isobaric surface.

REPORT ON HYDROGRAPHIC OBSERVATIONS AT A SERIES OF ANCHOR STATIONS ACROSS THE STRAITS OF FLORIDA*

By Albert Eide Parr,

Bingham Oceanographic Laboratory, Yale University

On its cruise No. 65, sponsored jointly by the Woods Hole Oceanographic Institution, and Bingham Oceanographic Foundation of Yale University, the research ship "Atlantis" made a series of five anchor stations across the Straits of Florida, from April 17 to April 23 in the locations indicated in fig. 1, between Fowey Rocks and Gun Key. Each station was occupied for 24 hours, with observations of temperatures and salinities taken in series down to a depth of 600 meters approximately every two hours; under the supervision of A. Woodcock, with the assistance of Y. H. Olsen and M. D. Burkenroad, and with the excellent cooperation of the ship's captain, F. S. McMurray, and the entire ship's company.

At his own suggestion, for which the author is greatly indebted, arrangements were also made by the chief mate, N. C. Kelly, to have surface velocity observations made by a taff-rail propeller log designed for sailing ships at slow speed; a usable current meter for deep-sea observations being unfortunately not available at the time.

The author also wishes to acknowledge his indebtedness to D. T. Pitcher, for his invaluable assistance in the graphical treatment of the data, and in the preparation of all illustrations for this report.

Unprotected thermometers were used at intervals to give accurate records of depth of observations; and the correction of depth and of temperatures, the titration of salinities and computation of densities (σ_t) were all carried out by A. H. Woodcock on behalf of the Bingham Oceanographic Laboratory according to the routine methods of the Woods Hole Oceanographic Institution.

For simplicity's sake, the anchor stations will in the following be designated by the numbers from *1* to *5* instead of 2854 to 2858, the numbers reading from left (west) to right (east) with reference to the direction of the current; and the 12 series of observations made at each station will be designated by the capital letters *A–L*.

* Joint contribution from Woods Hole Oceanographic Institution (No. 155) and Bingham Oceanographic Foundation, Yale University.

Figure 1. "Atlantis" anchor stations in Straits of Florida, 1937.

TEMPERATURE-SALINITY CORRELATIONS

The plotting of the temperature-salinity correlations serves a duplicate purpose: 1) to indicate the identity and relationships of the observed water masses, and 2) to disclose intrinsic evidence of probable errors of observation or transposition in the tables. The correlation curves for all series of observations are shown in figs. 2–6.

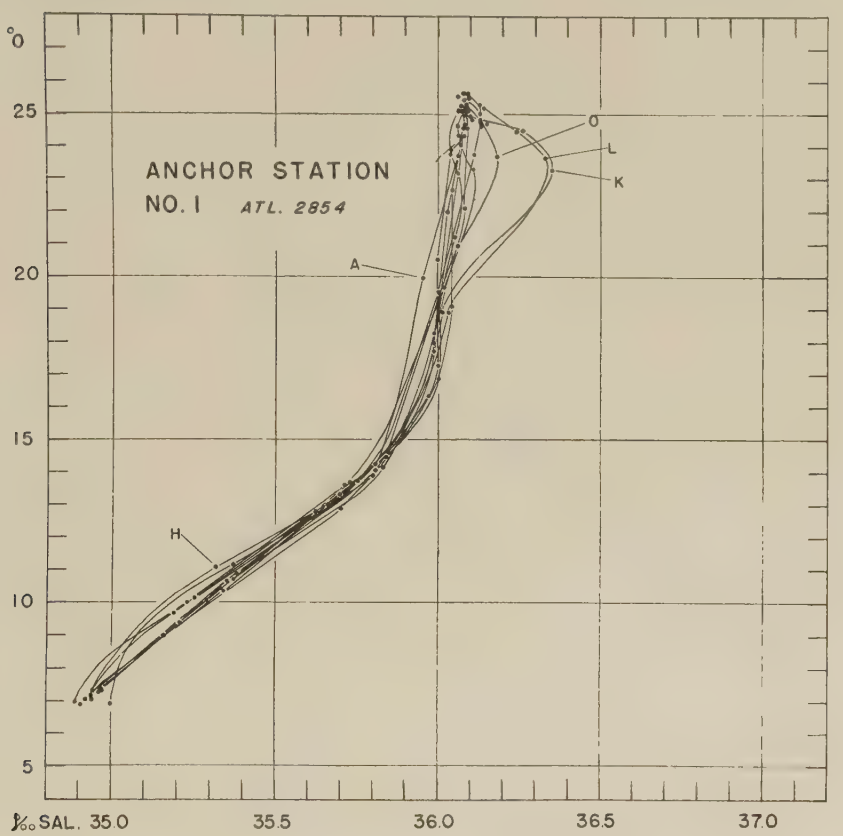


Figure 2. Temperature-Salinity correlations, Anchor Station 1.

Station *1* (fig. 2) shows a fairly uniform picture of water of Mexican Gulf rather than Caribbean type (see Parr, 1935). Two series, however (*K* and *L*), indicate an invasion of the edge of the Florida Current. None of the series gives any evidence of errors of observation or transposition.

Station *2* (fig. 3) gives the most varied picture, with waters of Caribbean type generally predominant, but with water of the type usually observed at station *1* appearing on two occasions (series *D* and *J*). In series *H* there is intrinsic evidence of a transposition of salinity records, and this possibility has been taken into consideration in the further use of the data.

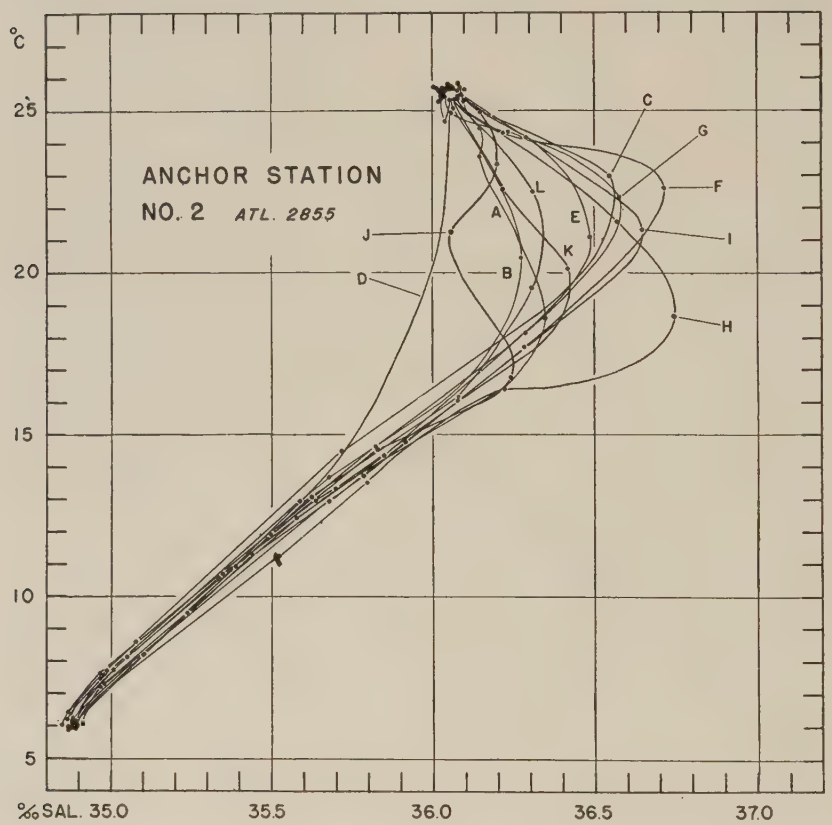


Figure 3. Temperature-Salinity correlations, Anchor Station 2.

The curves for anchor station *3* (fig. 4) also show considerable variation on a minor scale, but are all strictly within the Caribbean pattern.

The series made at anchor stations *4* and *5* are again very uniform, with anchor station *4* showing the least range of variation of all stations (figs. 5–6).

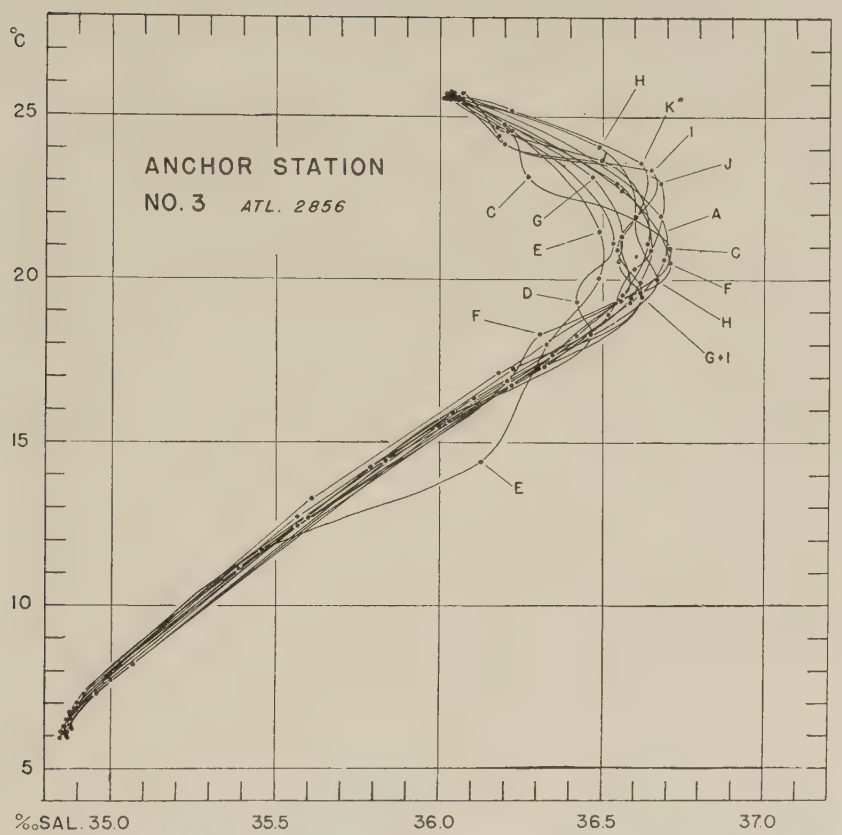


Figure 4. Temperature-Salinity correlations, Anchor Station 3.

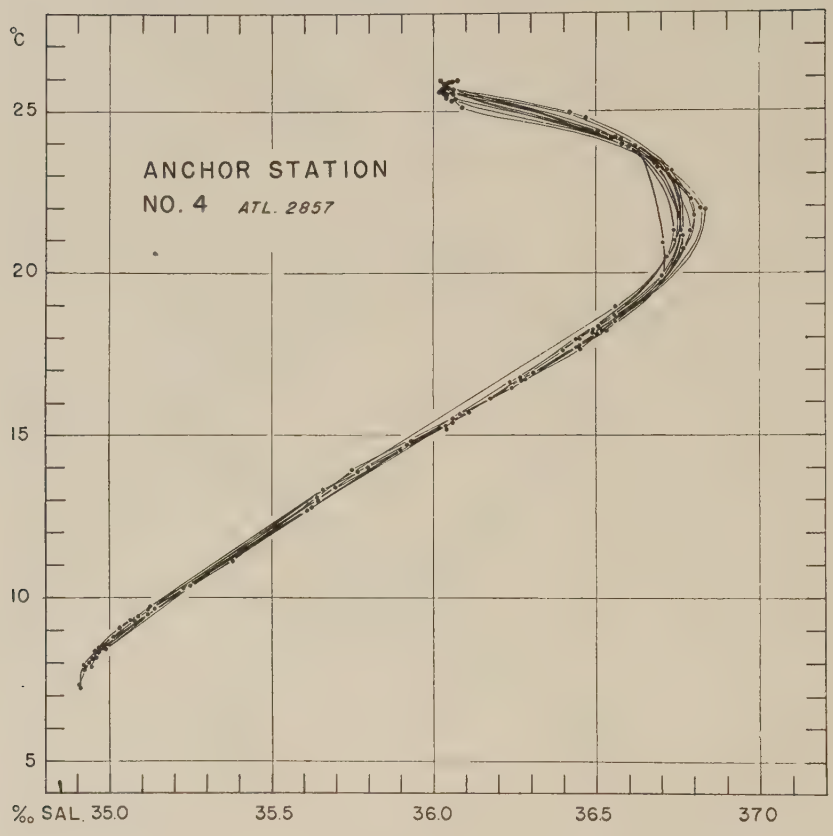


Figure 5. Temperature-Salinity correlations, Anchor Station 4.

Series *C* at anchor station *5* gives a good example of how errors in transposition, only, can be discovered and corrected by the use of the temperature-salinity correlation method. As given in the records of observation, this curve would take the form indicated by the dotted line (fig. 6), but it is evident that the almost identical salinities recorded from depths of 281 and 384 meters, temperatures of 17.99 and 16.41° C. must have been obtained by sampling the same bottle twice; that is, by moving the salinity series up one sample in relation to the temperature series. When correction for this error is made, the temperature-salinity curve for series *C* conforms perfectly with the curves for the other series as indicated by the open circles in fig. 6.

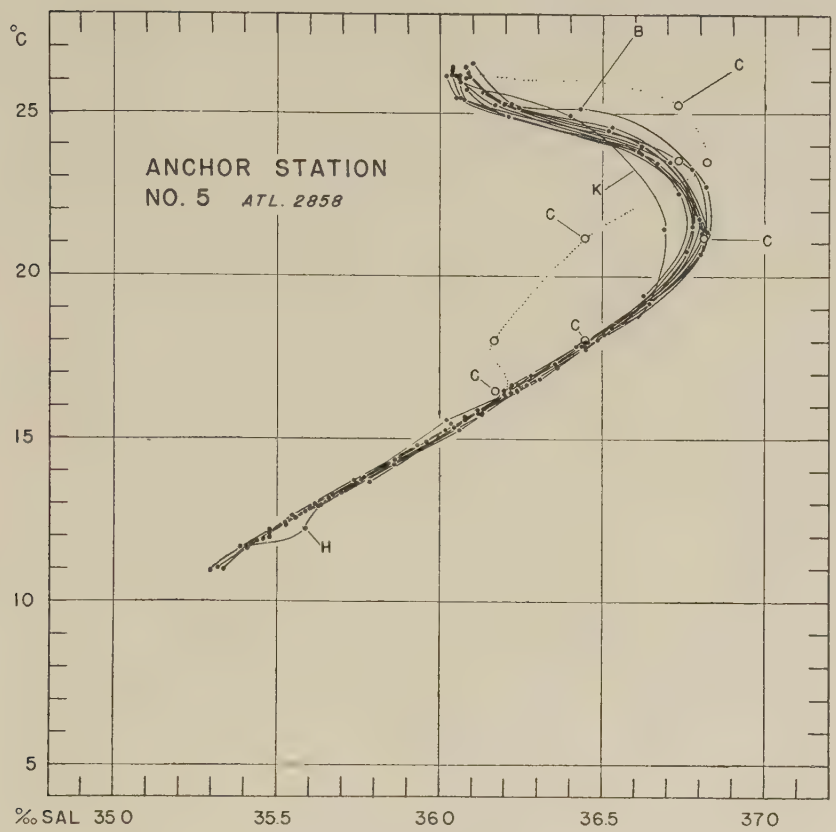


Figure 6. Temperature-Salinity correlations, Anchor Station 5.

DEPTH-TIME PROFILES

For the purposes of this report, only the time profiles of salinities will be presented, in view of the general correlationship between salinities and temperatures, of the fact that temperature profiles will not be made use of separately in this report, and that temperature variations will again find expression in the density-time profiles to be introduced later. The drawing of the salinity-time profiles (figs. 7–11) from the vertical salinity curves scarcely requires any explanation.

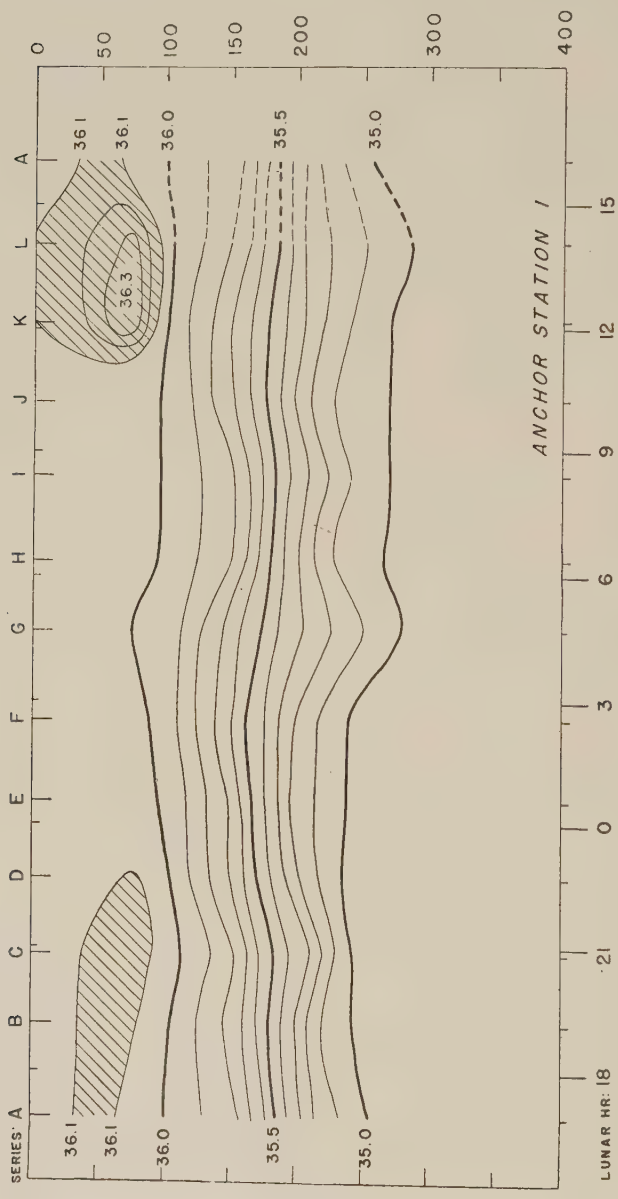


Figure 7. Salinity-Depth-Time profile for Anchor Station 1. Isohalines for every .010/oo salinity. Depths in meters on right. Time verticals of observation series (A–L) at top. Lunar time scale (Moons Transit = hour 12) at bottom.

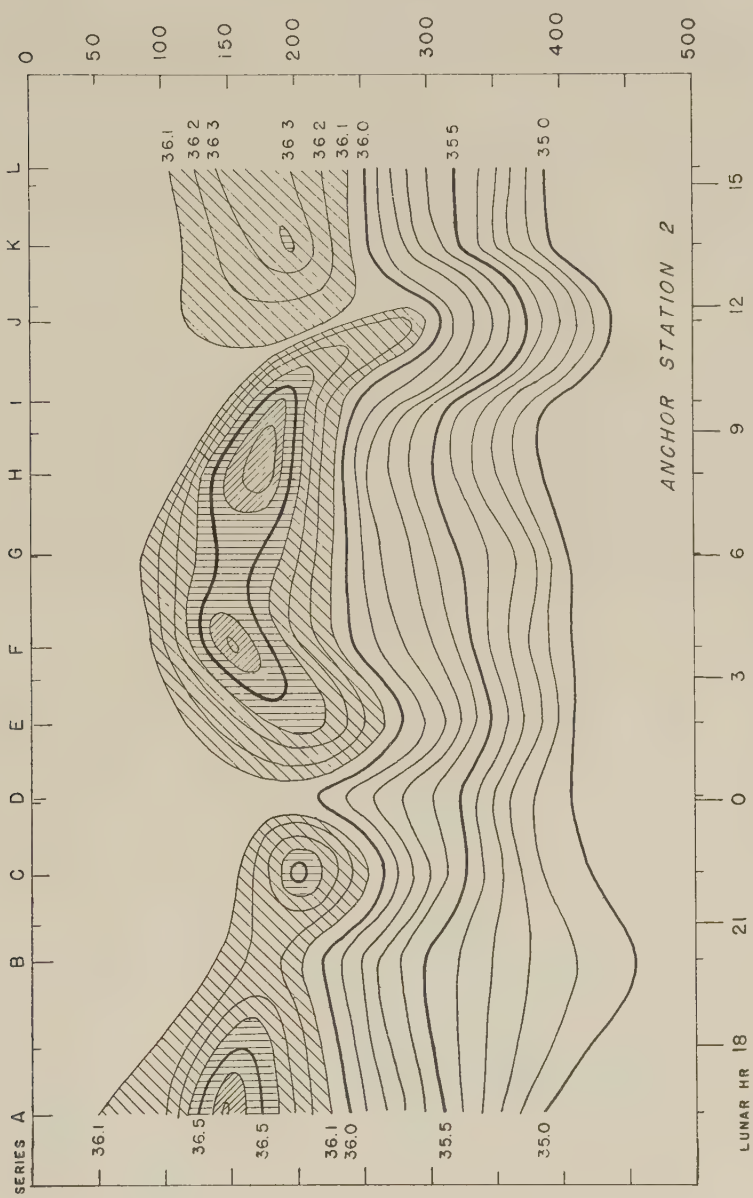


Figure 8. Salinity-Depth-Time profile. Anchor Station 2. See expl. fig. 7.

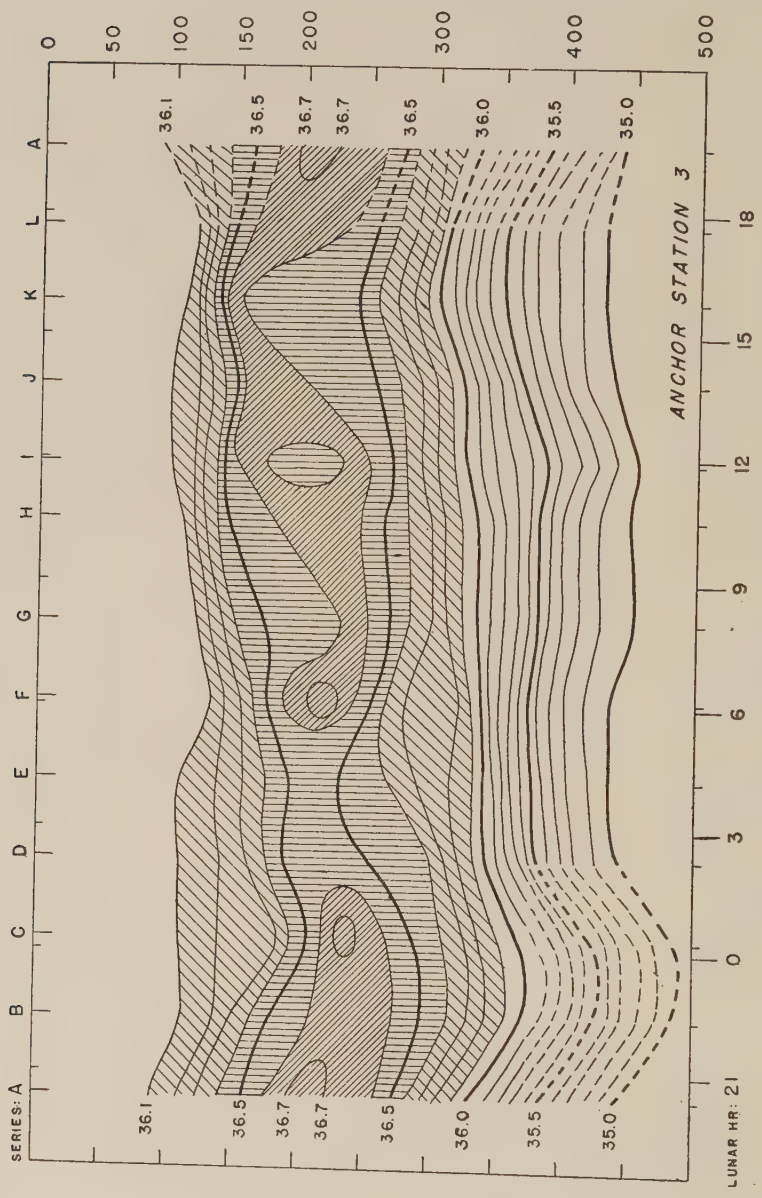


Figure 9. Salinity-Depth-Time profile. Anchor Station 3. See expl. fig. 7.

After the salinity-time profiles had been drawn, the extreme situation shown by series *D* at station *2* (fig. 8) was given the time designation of 0, and lunar hours were counted from this point and marked accordingly in the time profiles of all stations. This time schedule thus developed from the hydrographic observations alone, proved absolutely identical with the true lunar time schedule based upon the moon's transit (13 hr. 56 min.; series *J*, st. *2*, 13 hr. 28–33 min.; April 19, see fig. 8).

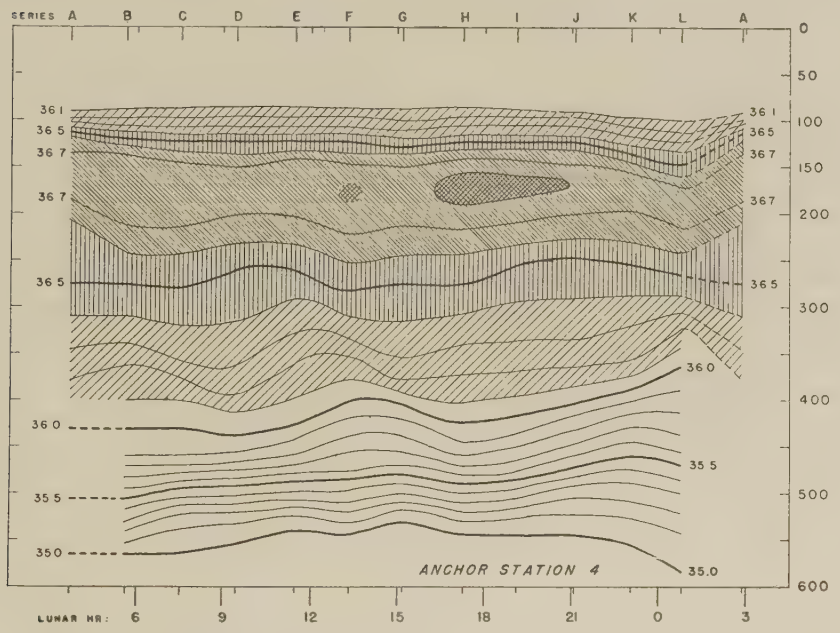


Figure 10. Salinity-Depth-Time profile. Anchor Station 4. See expl. fig. 7.

As we shall see later (p. 12), the disturbing peculiarities of series *J* at station *2* may find an intelligible explanation in the space profile for the corresponding lunar hour.

SPACE PROFILES

The salinity-space profiles for every three lunar hours shown in figs. 12–13 (pp. 14–17) were drawn on the basis of the isohaline intercepts with the corresponding time verticals in the depth-time profiles shown in figs. 7–11. The density zone between $\sigma_t = 25$ and $\sigma_t = 26$ is shown in hatching in every second profile for reasons to be explained later.

In the time sequence of these space profiles, we observe the indications of a very interesting hydrographic development. From the profile for the 0 hour to the profile for the 6th lunar hour an oblique extrusion develops through the

second station, extending upwards towards the first. In the 9th hour profile a beginning occlusion is indicated, and in the 12th hour profile this occlusion appears to have been completed, with a body of higher salinity to the left "leaning" obliquely against the boundary of higher salinities to the right, with lower salinities between.

In this profile for the 12th lunar hour, we see how the peculiar observations in series *J* at st. *2* can actually be intelligibly combined with the rest of the series. The picture indicated in the 12th lunar hour profile may be interpreted to show the inverted boundary of an extrusion just occluded.

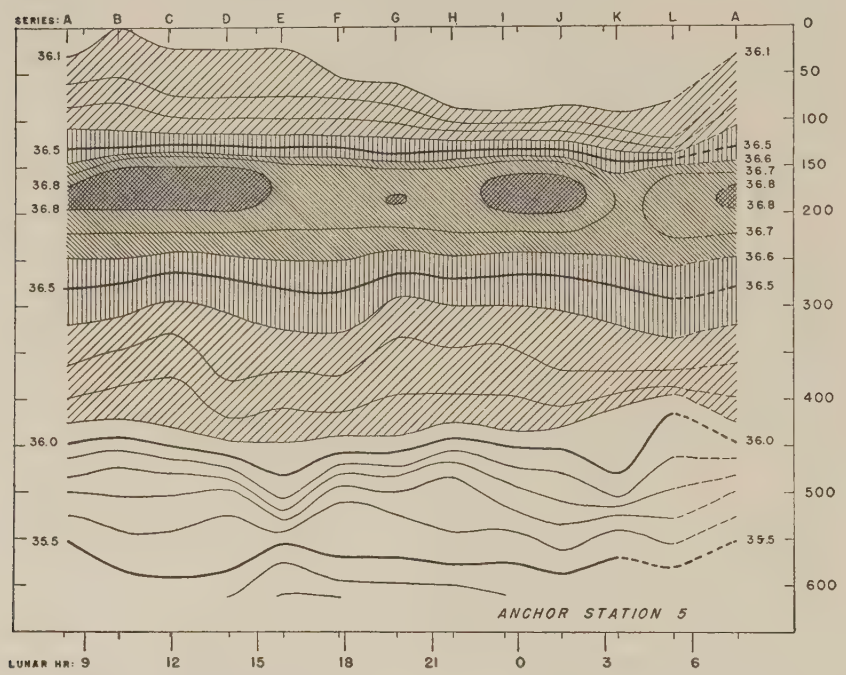


Figure 11. Salinity-Depth-Time profile. Anchor Station 5. See expl. fig. 7.

From the profile for lunar hour 12 to that for lunar hour 18, we see the formation of a new extrusion, but this again passes out of the picture for lunar hours 21–24.

With diurnal as well as semi-diurnal variations in the velocities at all depths recorded by Pillsbury (1886, 1887) from direct observations, this disappearance of the second extrusion from our profiles before its completion may well be due simply to its passage with the current through our lines of observation at an average velocity in relation to its rate of formation differing from the average velocity of passage of the first extrusion. On the other hand, it might also

indicate an aborted second extrusion. These possible interpretations will be discussed in greater detail in the following chapters. At the bottom of the series of lunar hour space profiles one will find a corresponding series of diagrammatic drawings suggesting a two-dimensional horizontal interpretation of the vertical profiles on the assumption of the passage through our line of observation of one extrusion formed every twelve lunar hours (see p. 48).

PERIODICITY OF VARIATIONS

The question of the finer details of periodicities in the profile here discussed is so complicated by the occurrence of special oceanographic events during the period of observations, that it can only be dealt with in a preliminary fashion with regard to its grossest general features, until more data may be made available through future research.

When the profiles for selected lunar hours shown in figs. 12–13 were drawn on the basis of a lunar synchronization of the values found from the time profiles shown in figs. 7–11, we started quite simply by assigning the number 0 to the most extreme situation (series *D*) shown at the most variable station (*2*), counting lunar hours from this point without consideration of the actual lunar time. When the time schedule thus developed from the empirical hydrographic data proves to be absolutely identical with the true lunar time schedule based upon the moon's transit during the days of observation, this may of course be only a very fortuitous coincidence, but with no evidence to confirm this possibility it would be extremely unreasonable to base our discussion on such as assumption.

As it is, the extreme situation shown by series *D* at station *2* proves to have occurred exactly at the hour 0 or 24 of the lunar day, and the repetition of this extreme situation in a somewhat modified form immediately after series *J*, at lunar hour 12 in our hydrographic time schedule coincides exactly with the time of the moon's transit.

Without any evidence to the contrary, the only reasonable conclusion to be drawn from these facts is that the variations observed at station *2* must in a large measure be under the control of lunar forces, at least with regard to the time of their occurrence.

It may further be seen from fig. 14 (p. 18) that the variations in maximum salinity at station *2* may very easily be combined in a curve showing a distinct period of six lunar hours as well as the 12 hour period.

In the surface salinities for station *2*, however, only a period of approximately a full lunar day is rather vaguely indicated, but neither surface salinities nor maximum salinities at any other of the stations here reported upon can be claimed to give any very plain evidence of regular periodicities in their variations.

Since any correlation with lunar influence is a correlation with a variable

(*Turn to page 20*)

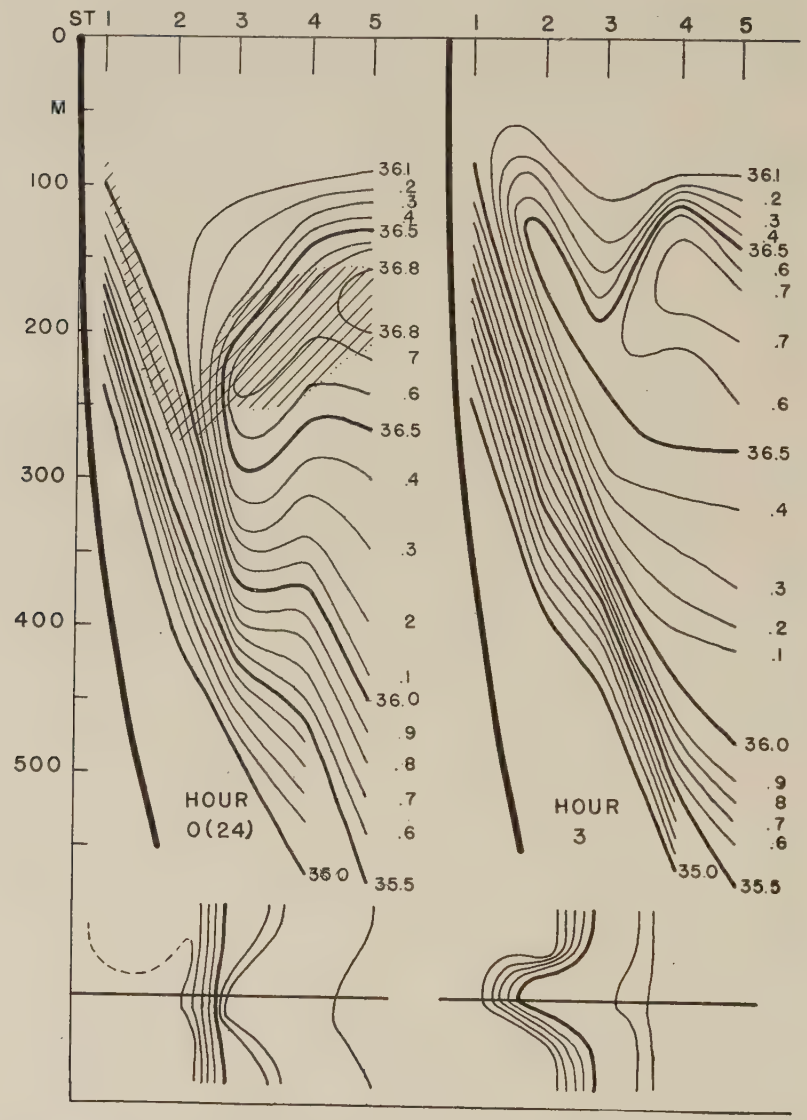
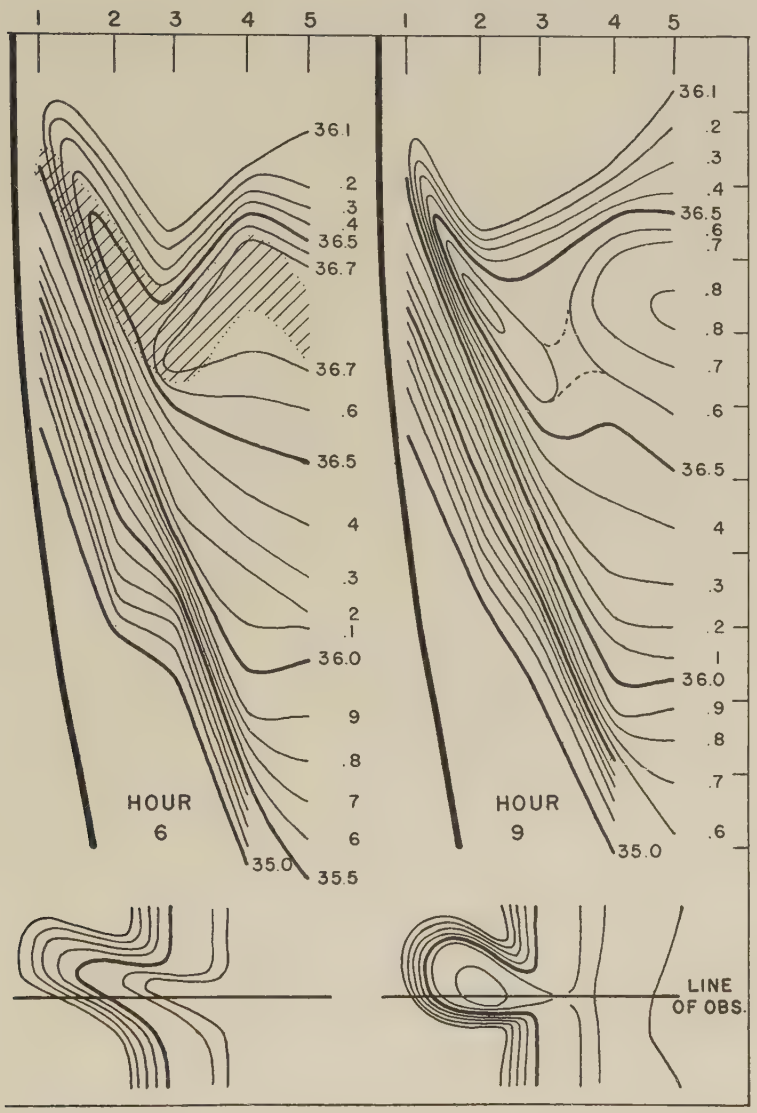


Figure 12. Space profiles of salinities for every three lunar hours from hour 0 to hour 9.



Density zone for σ_t 25 to σ_t 26 indicated by hatched area in every second profile. Diagrammatic horizontal Interpretation below each profile.

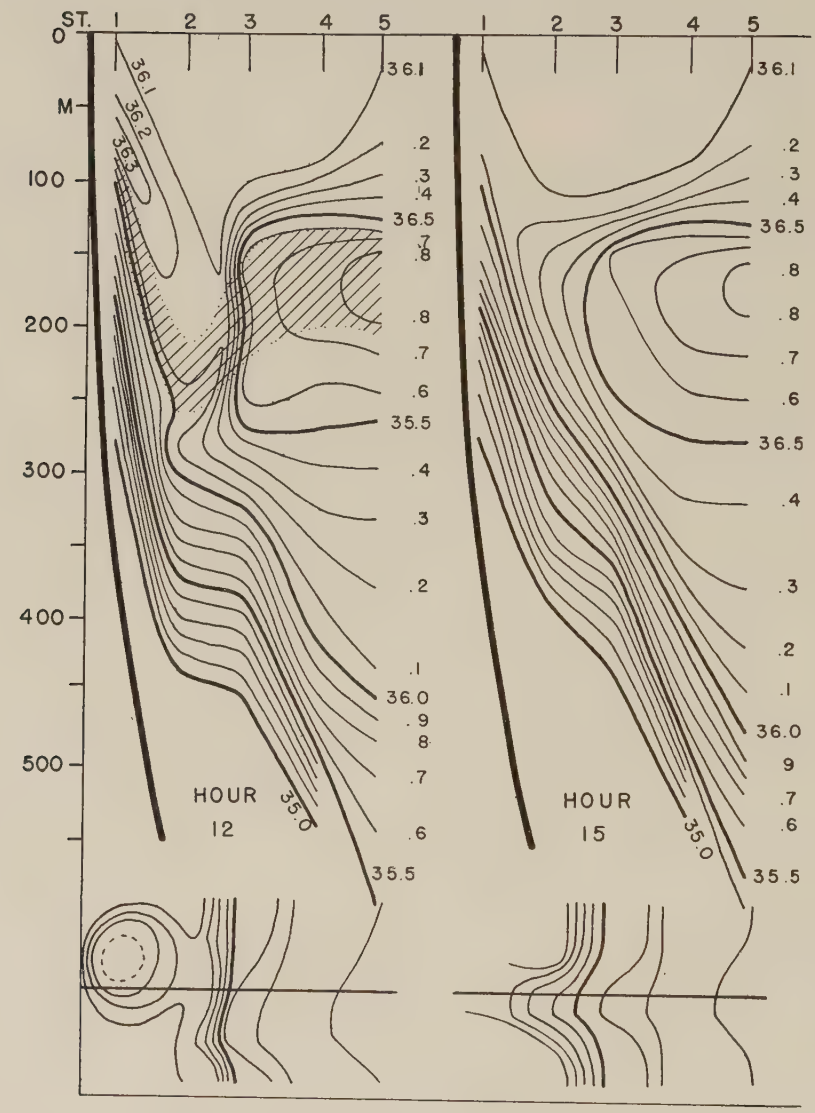
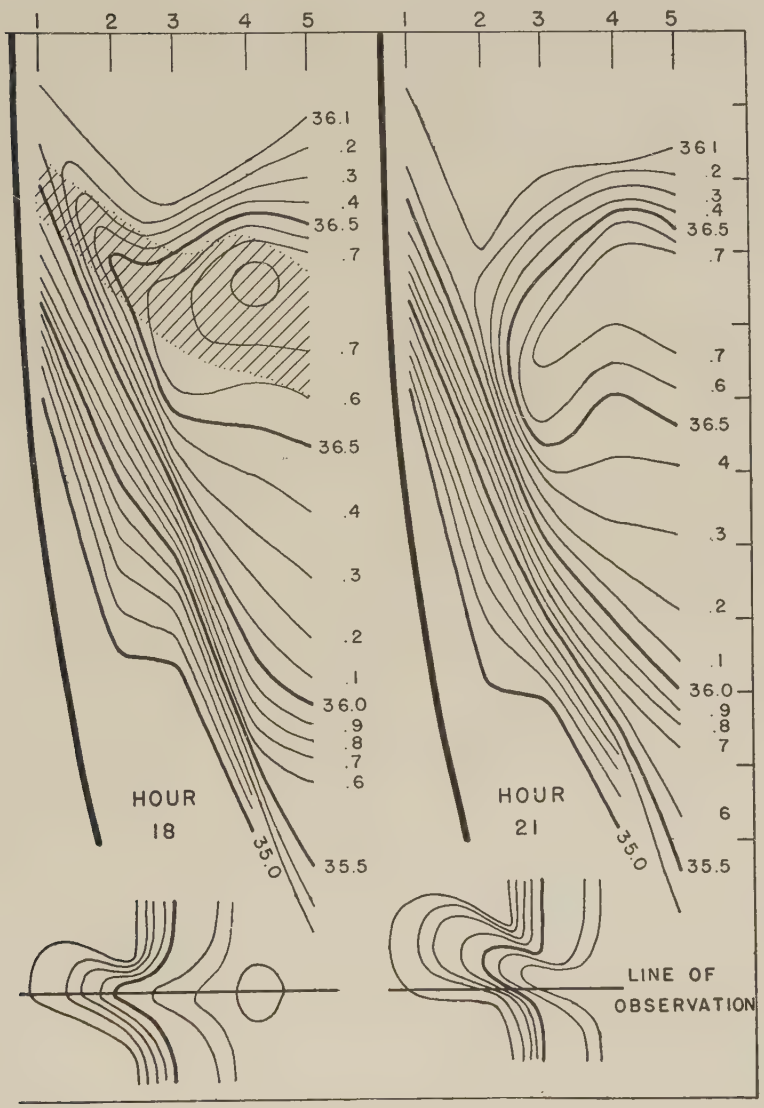


Figure 13. Space profiles of salinities for every three hours from hour 12 to hour 21.



Density zone for σ_t 25 to σ_t 26 indicated by hatched area in every second profile. Diagrammatic interpretation below each figure.

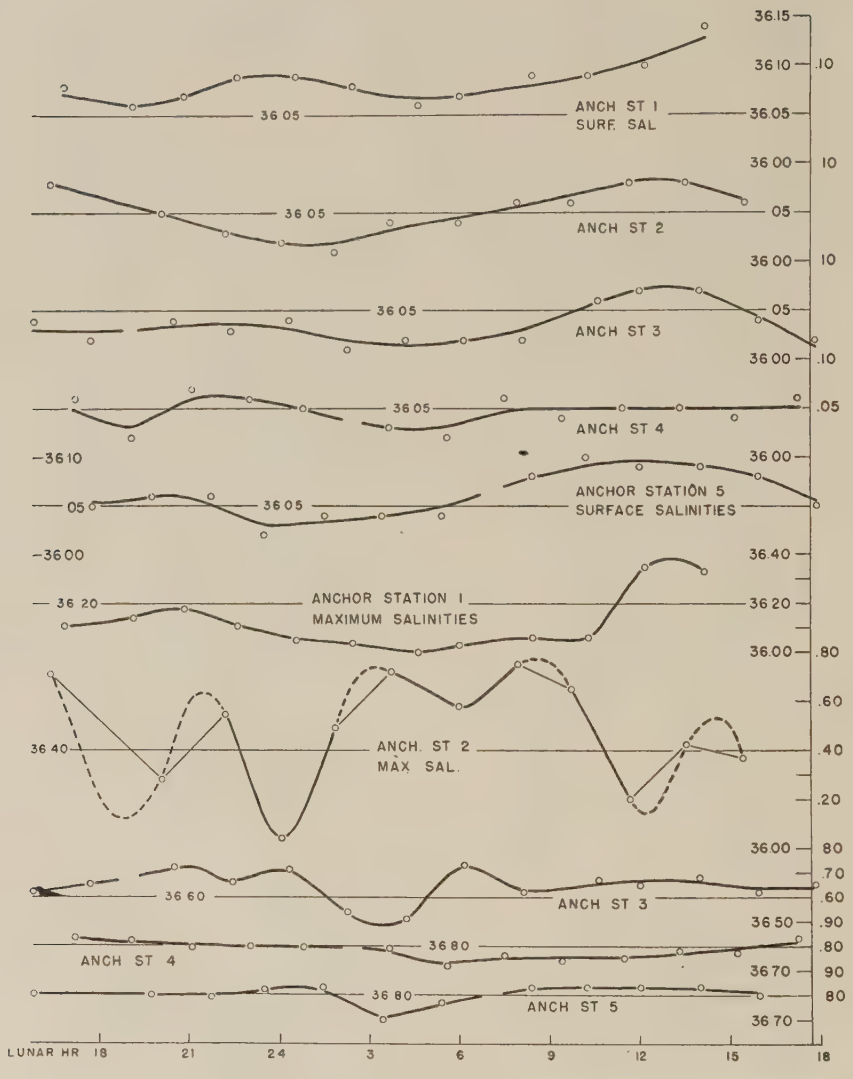


Figure 14. Variations in point of lunar time of surface salinities and of maximum salinities.

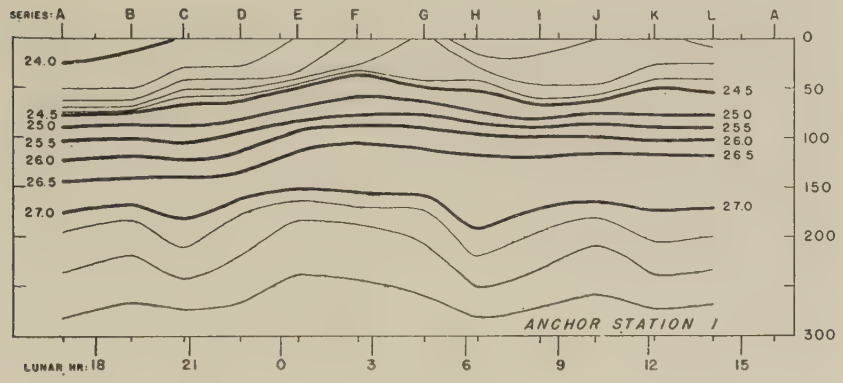


Figure 15. Density Depth-time profile for Anchor Station 1. Light lines for every .1 above σ_t 27.0 and below σ_t 2.45.

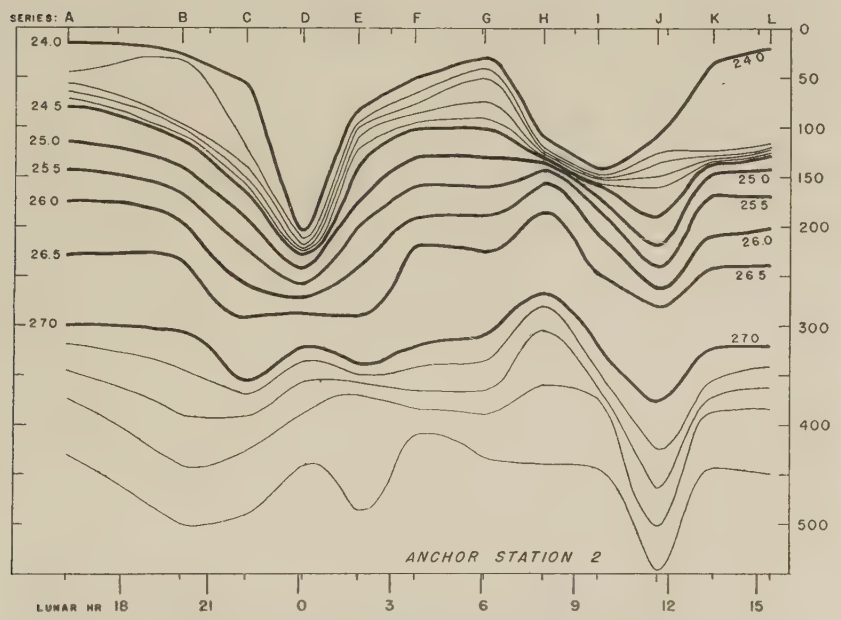


Figure 16. Density Depth-time profile for Anchor Station 2. See expl. fig. 15.

force, however, it would *a priori* seem more logical to look for the expression of such a correlationship in the calculated potential energies and velocities, rather than in such static quantities as salinities and temperatures, in which the variations are not only dependent upon the variable force but also upon the variability of the materials available for this force to operate upon. One might then first look to the variations in the density profiles (figs. 15–19) as an expression of variations in the distribution of mass, and thereby of potential energy. In the density profiles there is actually a fairly distinct indication of a 12 lunar hours period in the upper 200 meters at both stations *1*, *2* and *3;* with the deepest depression of the isopycnals around lunar hours 18–21 and 6–9 at station *1*, at hours 24 and 12 at station *2*, and at hours 6–9 and 18–21 at station *3*. Stations *4* and *5* show no distinct periodicity with reference to lunar time.

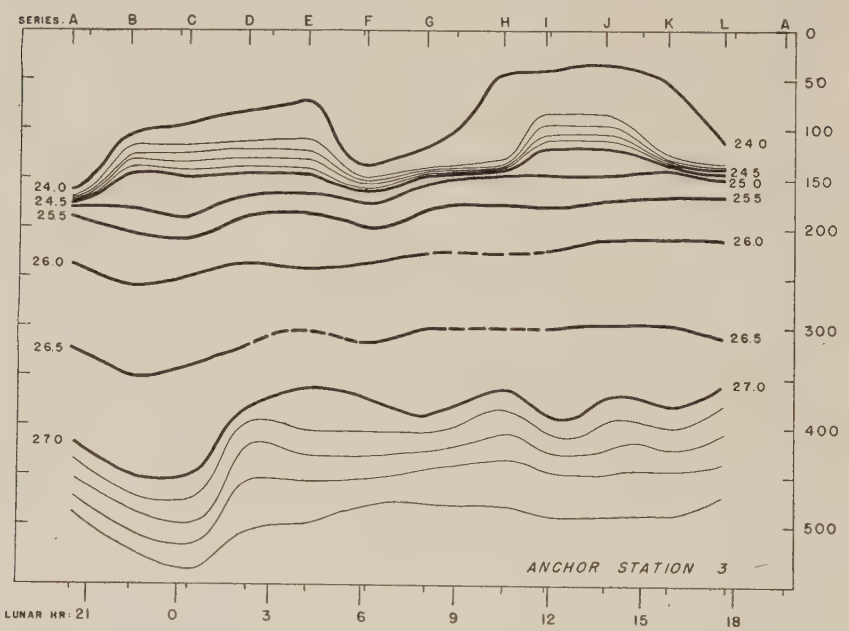


Figure 17. Density Depth-time profile for Anchor Station 3. See expl. fig. 15.

The next comparison could then be made with the variations in relative dynamic height shown in figs. 20–21. Here station *1* indicates both a 12 lunar hour period, with maximum relative elevation of the surface at hours 18–21 and 6–9, and a 24-hour period with maximum elevation at hours 18–21. Sta-

tion *2* again shows sharply the 12 lunar hour period with the maximum around hours 24 and 12; while stations *3*, *4* and *5* give no clear evidence of regular periodicities, the periodicity appearing in the density distributions in the upper levels at station *3* being offset by opposite variations below.

A study of the variations in surface velocity in which all variations in mass distribution are integrated, also brings out again very sharply the 12 lunar hour period in the intervals dominated by the second station (intervals *1–2* and *2–3*), while a consideration of the third and fourth station intervals combined gives some indication of a 12 hour period with maximum velocities around lunar hours 3–6, and 15–18.

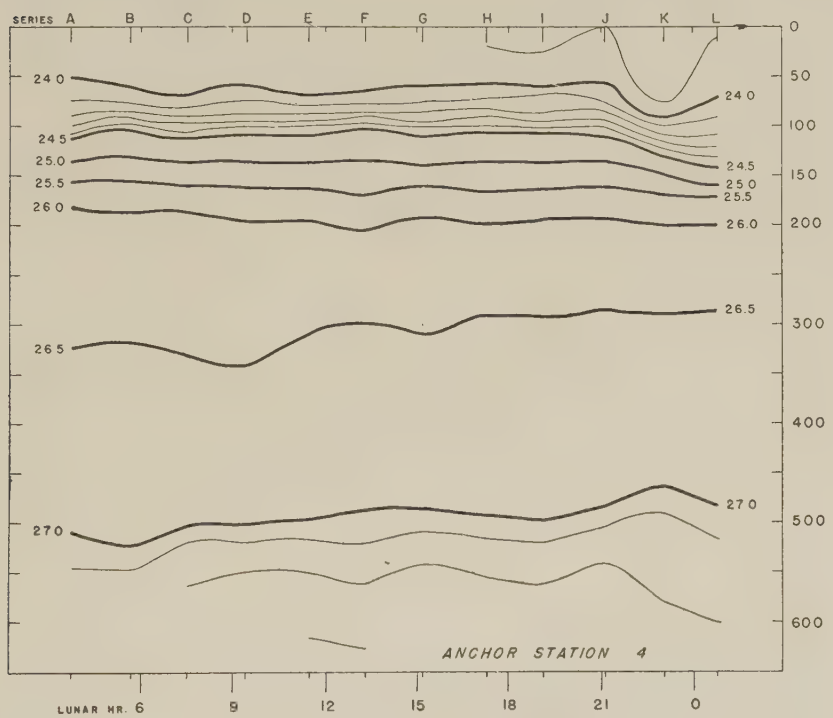


Figure 18. Density Depth-time profile for Anchor Station 4. See expl. fig. 15.

Finally, the direct current observations from the same profile reported by Pillsbury (1886, 1887) show such pronounced semi-diurnal, diurnal and monthly variations with reference to lunar time that there can scarcely be any reasonable doubt that lunar forces play a very important role in the hydrodynamic condi-

tions in the Straits of Florida (see also fig. 27, p 40). Under normal circumstances it would now be logical to attempt to delve more deeply into the problem of these lunar periods, and this we may hope to do at some later date when more material may have become available. But in spite of the importance of the tidal factors, it is evident that in the observations here reported upon the

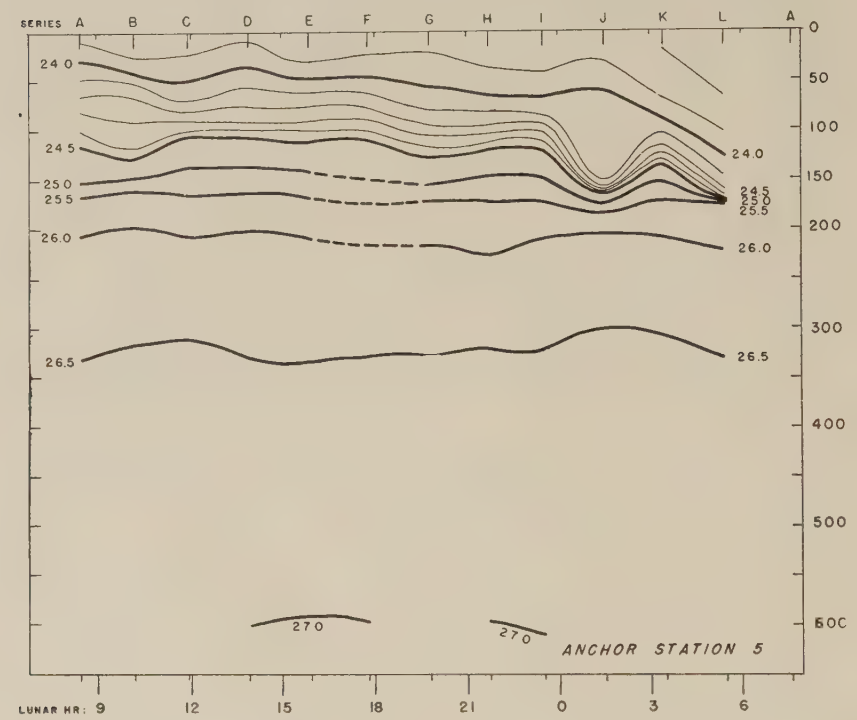


Figure 19. Density Depth-time profile for Anchor Station 5. See expl. fig 15.

picture has become greatly distorted by the influence of other probably still greater forces, and in the ensuing hydrographic confusion it seems advisable to limit our consideration of lunar periods to the preceding general remarks, and to turn our attention to the effort of finding at least a possible interpretation of the events which may have been taking place while these observations at the "Atlantis" anchor stations were made.

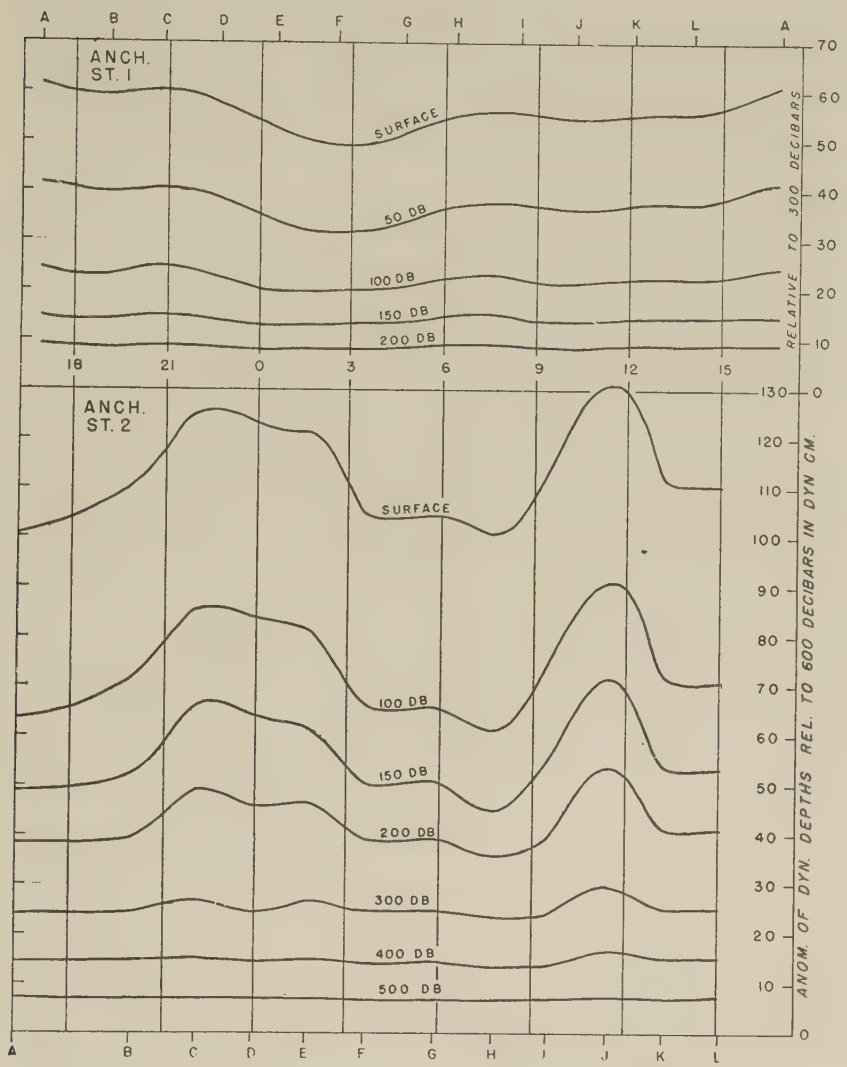


Figure 20. Variations in dynamic height relative to 300 decibars at Anchor Station 1 (above) and relative to 600 decibars at Station 2 (below). Time-verticals for every 3 lunar hours, marked in centre. Time-verticals of observations marked by capital letters above (St. 1) and below (St. 2).

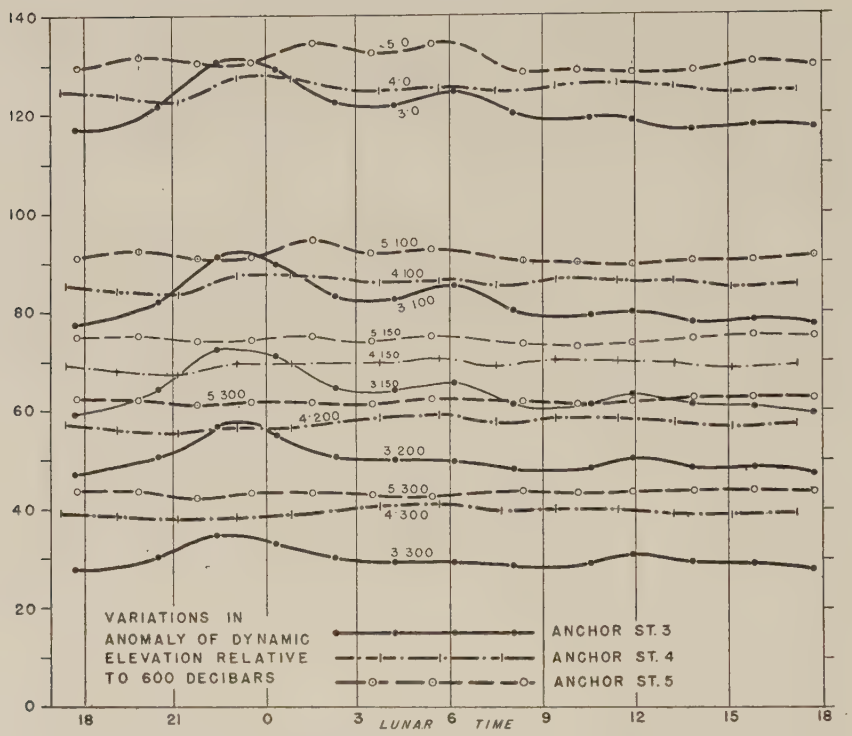


Figure 21. Variations in dynamic heights relative to 600 decibars at Anchor Stations 3–5 Station number, isobar surface and times of observation indicated on each curve. Scale of anomalies in dyn. cm. at left.

DYNAMIC ANALYSIS

For the following considerations dynamic heights have been calculated by the routine methods, using Sverdrup's simplified procedure (Sverdrup, 1933), and only one point may require particular mention here.

Since observations at the first station do not extend beyond the 300 decibar level, it was necessary to make extrapolations from the other stations to determine the height of this isobaric level relative to the 600 decibar surface which has been used as the reference level for the other stations. To do this, the slope of the 300 decibar level across the Straits was plotted for every three lunar hours according to the system used for plotting the transverse profiles and the time space projections on pages 14–17 and 50–51. The slopes were then extended from station *2* rectilinearly to station *1*. This procedure may be justified by the entirely similar slopes shown by the 200 decibar surface relative to 300 decibars which was observed both at station *1* and station *2* and which are

also entered in our figure 22. This rectilinear extrapolation gave a range of variation in anomaly of relative dynamic height of the 300 decibar surface relative to the 600 decibar surface at station *1* of 13.5 to 26 dynamic centimeters, there being only one value above 19.8 dyn. cms., however, and this value may be abnormal based upon special conditions at station *2* at this time. The average extrapolated dynamic elevation of the 300 decibar surface at station *1* was 19.2

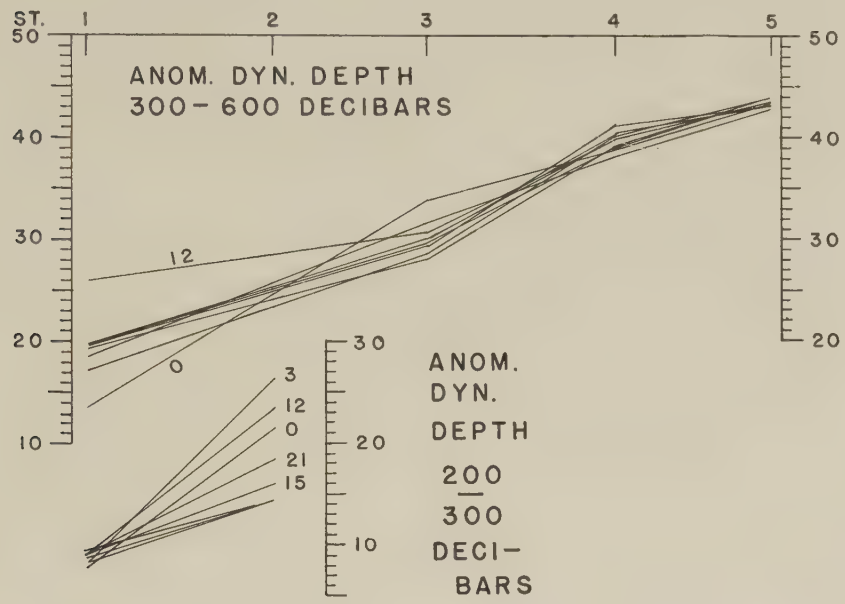


Figure 22. Profiles of dynamic heights of 300 decibar surface relative to 600 decibars used for extrapolations to Anchor Station 1.

dyn. cms., and no less than five of the eight extrapolated values were within ± .7 dyn. cms. In the further use of the extrapolations for the purpose of studying calculated velocities and so forth (see page 35) both the individual extrapolated values and the average values were used for comparison. It was found in most instances that the difference between use of the two values was too slight to be of any significance (see table on page 37).

METHOD OF ESTIMATING VOLUME TRANSPORT AND AVERAGE VELOCITIES

While attempting to make volume transport estimates by the customary planimetric method of computation from fully drawn velocity profiles, the writer has felt considerably disturbed by the amount of uncertainty which

must always attach to the values derived by this procedure. Two main sources of probably errors, which commonly tend to become systematic and therefore cumulative, are obvious; one referring to the plotting of the velocity profile, and one to the planimetric evaluation. In plotting the velocity profile one generally assumes the average velocity calculated between two stations to occur in the mid-vertical of the station interval. This would be strictly correct only if all lines of equal velocities should run parallel and the vertical velocity gradient should be entirely uniform; but would otherwise only be correct under very special circumstances. If the slope of the velocity lines is fairly uniform throughout, the method may perhaps nevertheless suffice in first approximation, although it will generally tend to introduce a systematic error, dependent upon the changes in the vertical velocity gradient. But when sharp inflections occur in the lines of equal velocity between the station interval under consideration and the next adjacent station intervals on either side, this obviously implies that the depth of a certain average velocity calculated in the central column, is not, under otherwise equal circumstances, the depth at which this velocity occurs in the middle of the column, but a depth which must be once or twice intercepted by the velocity line in question at some other point or points than the middle of the station interval in which it is calculated.

A situation of this sort is illustrated in fig. 23. It must be remembered that the calculated velocities are the average velocities between the two stations, and it is then obvious that if, for instance, an average velocity of 15 cm. sec. had been calculated to occur at level *A–B*, and we then drew this velocity line so as to intercept the mid-vertical at this level (as it is now intercepted by the 20 cm. sec. velocity line in our figure) our profile would show 15 cm. sec. as the maximum instead of the average velocity at this level, and a very serious systematic error would be introduced in the planimetric estimation of volume transport. The very uncertain process of free-hand interpolations to attempt to achieve correct average values must therefore be resorted to, and this also further implies the free-hand extrapolation by sheer guesswork of probable maximum velocities higher than any of those obtained by the calculation of average velocities. This latter point has already been clearly stated by Wüst (1936, p. 54) who emphasizes the fact that calculated velocities always represent minimum values, tending to deviate farther from the true velocities with increasing station distances.

While these difficulties in plotting a true velocity profile may to some extent be overcome by the intelligent subjective evaluation of the degree to which these various considerations are involved, it would seem obvious already that (confluent) velocity profiles are not a very suitable and accurate basis for the estimation of volume transport. Nevertheless, still further difficulties and objections to the method are to be found in the next step of the process, namely the planimetric evaluation of the profile.

The main difficulty is here again of similar character to that inherent in the

plotting of the profile, and it arises from the fact that when the ribbon of the velocity integral to be evaluated planimetrically diverges from a straight course, this divergence will under otherwise equal conditions change the actual average velocity of the ribbon from the arithmetic mean of its limiting values towards that limiting value which is farthest away from the center of inflection, i. e., which takes the outside curve. This can be most clearly shown by a situation such as that at the lower inflection point of the main current velocity

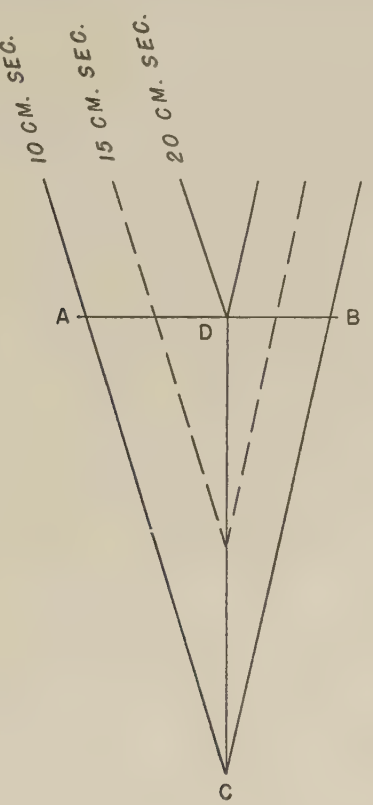


Figure 23. See text.

curves in any current profile. If for simplicity's sake we draw the velocity lines in polygonal form and assume that the arithmetic mean velocity occurs midway between the limiting velocities, and now consider the velocity distribution in the bottom triangle, e. g., of the velocity ribbon between 10 and 20 cm. sec. as shown in figure 23; we immediately see that velocities higher than the arithmetic mean (15 cm. sec.) only occupy one-fourth $\left(\frac{1}{2}\times\frac{AB}{2}\times\frac{CD}{2}\right)$ of the

area of the entire velocity triangle $A\,B\,C$ ($\frac{1}{2} \times AB \times CD$). That is, the actual average velocity of the triangle will be more nearly 12.5 cm. sec. than 15 cm. sec. Since a precise evaluation of this factor by the use of the planimetric method is beyond feasibility, it must remain one of the permanent sources of error in this procedure, and that a complete disregard for this source of error may lead to very significantly erroneous results may be shown by the fact that a difference of over 16 per cent developed by an experimental estimation of the volume transport of the 1933 Caribbean profile recorded in table I arrived at with and without consideration of this factor.

It is clear that all the difficulties both in plotting the velocity profile and evaluating it in terms of volume transport arise from the effort to obtain a true, integrated picture by interpolation and extrapolation from average values calculated only for larger intervals. One very logical way to avoid these difficulties by presenting the calculated average values strictly for what they actually are, by the histogram method of drawing the velocity profile, has already been introduced and well argued by Wüst (1936, p. 54). It is evident that this histogram method of procedure when used as a basis for volume transport estimates is free from the errors of the continuous velocity profile calculations and will give a strictly correct result, in so far as the velocity equation is applicable to the region investigated.

It is also evident, however, that all the difficulties encountered in the continuous profile method arise from the uncertainty about the exact values of the horizontal distance (L) when interpolations between the various station intervals have been resorted to. But this distance (L) is actually not a factor in the calculation of volume transport as the following considerations will show.

The volume transport between two station verticals is of course expressed by the equation:

$$Tr_{(m.^3\ sec.)} = v_{(cm.\ sec.)} \times L_{(km.)} \times D_{(m.)} \times 10$$

where v is the average velocity of the column expressed in cm. sec., L the station distance expressed in kilometers, and D the height (depth) of the column expressed in meters.

But according to Bjerkness' equation:

$$v_{(cm.\ sec.)} = \frac{h_1 - h_2}{2\omega \sin \varphi\, L} \times 10^3$$

in which h^1 and h^2 stand for the average dynamic height of each station vertical expressed in dyn. cm. Therefore:

$$Tr_{(m.^3\ sec).} = \frac{h_1 - h_2}{2\omega \sin \varphi\, L} L \cdot D \times 10^4$$

or:

$$Tr_{(m.^3\ sec.)} = \frac{h_1 - h_2}{2\omega \sin \varphi} D \times 10^4$$

From this we see that the cumbersome velocity calculation and plotting, and the planimetric estimate of the profile can be omitted entirely in obtaining an estimate of volume transport between two stations.

The simple method of estimating current transport suggested by this equation has actually been available to oceanography for a considerable time. A related equation was first presented by Ekman (1929) and subsequently by different method of derivation and in a different presentation by Werenskjold (1935). But since it does not seem to have received the wide usage it deserves, the writer would like to summarize briefly its great practical advantages over the planimetric method, or even over the histogram method of Wüst.

The *first* great advantage derives from the fact that since the station distance L has disappeared from the equation, it is evident that the net volume transport through an entire profile can be determined quite simply from the difference in dynamic height between its two extreme stations, without any assumption of rectilinear slope, since the sum of all differences in height (or any other coordinate) in successive integrals of a continuous curve must add up to the difference between its two end points, regardless of the actual form of the curve. In table I a sample is given of a complete calculation of volume transport through a Caribbean profile (which will be of subsequent use in this report), in which direct calculations from the end stations only are compared with the calculations based on the values for every separate station interval according to the histogram method of Wüst. The data will be seen to agree within the error of such computations as this, and it should be remembered that the greatest accuracy attaches to the direct estimate from the end stations, the deviations shown by the value obtained by integration of all station intervals being due to the numerous additional calculations required to arrive at this figure (for experimental comparison of practical accuracy the estimates of volume transport in the different station intervals has been based upon a complete calculation of average velocities, instead of upon the much simpler method of using the above equation, also for the separate station intervals, as well as for the total profile).

Secondly, the fact that direct calculations of volume transport from the hydrographic differences between the end stations only is even more reliable in practice, since it is simpler while at the same time equally accurate under ideal conditions, removes all reason for apprehension with regard to whether a sufficient number of fortunately located stations are available or not.

Third, the equation obviates the necessity of interpolated velocity calculations over a sloping bottom between a shallower and a deeper marginal station, in which calculation the actual magnitude of L becomes a factor of great un-

TABLE I. VOLUME TRANSPORT THROUGH THE CARIBBEAN (PROFILE 1B) CALCULATED DIRECTLY FROM END-STATIONS AND BY STATION INTERVALS FROM COMPUTED VELOCITIES

Depth Decibars	Station 1515 Anom. Dyn. Depth Dyn. Cm.	Station 1515 Anom. Dyn. Height Dyn. Cm.	Weight (50 decibar units)	Station 1505 Anom. Dyn. Depth Dyn. Cm.	Station 1505 Anom. Dyn. Height Dyn. Cm.
0	0.0	185.0	× ½	0.0	143.5
50	18.7	166.3	× 1	15.8	127.7
100	36.3	148.7	× 1	28.3	115.2
150	51.9	133.1	× 1	37.2	106.3
200	64.9	120.1	× 1½	42.8	100.7
300	84.2	100.8	× 2	57.7	85.8
400	99.1	85.9	× 2	69.0	74.5
500	111.8	73.2	× 2	79.4	64.1
600	122.6	62.4	× 2	88.7	54.8
700	132.7	52.3	× 2	97.6	45.9
800	141.4	43.6	× 3	105.6	37.9
1000	156.2	28.9	× 4	118.1	25.4
1200	169.9	15.1	× 5	128.4	15.1
1500	185.0	0.0	× 3	143.5	0.0
Aver. Anom. Dyn. H. 0–1500 Decibars		59.715	30		50.433
Aver. An. Dyn. H. St. 1515–St. 1505				9.2817 dyn. cm.	

St. 1515 17° 57′ N. St. 1505 11° 49′ N.
Aver. Lat. 14° 53′ N. Av.: $2\omega \sin \varphi = 3.75$

Volume transport: $\frac{h_1 - h_2}{2\omega \sin \varphi} \times 10^4 \times D = \frac{9.2817}{3.75} \times 10^4 \times 1500$
$= 37{,}127{,}000$ m.³ pr. sec.

Station Interval	Σ v . D 10^3m.³ sec.
1505–1506	−10,723
1506–1507	+ 1,064
1507–1508	+ 3,228
1508–1509	+33,347
1509–1510	−11,051
1510–1511	+ 9,093
1511–1512	− 4,305
1512–1513	+13,408
1513–1514	+ 25
1514–1515	+ 2,253

Total m.³ sec. $+ 36{,}340 \times 10^3$
$= 97.88\%$ of direct estimate

certainty,[1] while the dynamic height at the shallower station, which is the only quantity considered in the volume transport equation, can be fairly reliably determined by the method of Helland-Hansen and Nansen (see Helland-Hansen, 1934, pp. 270–272).

Fourth, it has been shown by Werenskjold (1935) that in the case of a coastal current of triangular profile its volume transportation can be calculated from a single station near shore, if the lower limiting isopycnal surface of the current is known, or can safely be assumed, to rise to the free surface of the ocean farther off shore. This reasoning is obviously also applicable in reverse to calculations from a station on the offshore side of a current, when the lower limiting isopycnal surface of the current is known to rise to the free surface between this station and the shore.

Fifth, the equation permits evaluation of the volume transport significance of variations in hydrographic conditions observed at the *same* station at different times without requiring the availability of simultaneous observations at other points, since h_1 and h_2 may equally well represent dynamic height at different times as in different locations.[2]

[1] Below bottom depth at the shallower station one must use the actual horizontal distance from the bottom to the deeper station vertical to represent the magnitude of L in the denominator of the velocity equation.

[2] To evaluate volume transport significance of variations observed at "Atlantis" station 2639, Seiwell (1937, pp. 31–34) resorts to a comparison with another station made four years earlier, a procedure which would be made quite unnecessary by the method here suggested. Taking the figures as recorded by Seiwell, the variations at station 2639 compared with themselves alone indicate potential variations in volume transport of 4.5 million m^3 per sec. which is certainly not a startlingly high value over such a great depth (2000 meters) as that considered in Seiwell's calculations. In making such a comparison, one must also always keep in mind that when vertical oscillations of internal boundaries occur these are most likely to be associated with vertical oscillations also of the *O* velocity level. Over infinite bottom the expansion of the lower layers causing a negative variation in dynamic height and a positive variation in higher boundary surfaces should in the absence of special forces, also mean a retardation of these lower layers (see Parr, 1937 c) with an upward movement of the *O* velocity level. Conversely a contraction of the lower layers should under the same circumstances mean a lowering of the *O* velocity level. If, on the other hand, the variations are due to bottom topography in a finite ocean, these relationships are likely to be reversed. Finally, the relationship between oscillations of isopycnal surfaces and vertical movements of the *O* level must generally be opposite for stations on opposite sides of the main current. The effect of the vertical oscillation of the *O* velocity surface associated with the vertical oscillations of the isopycnals may thus have to be added to or substracted from the variations in volume transport calculated with reference to a fixed datum level, dependent upon the special circumstances of each particular case.

Sixth, transport equations of the form above given or of similar form provide opportunity for plotting the horizontal distribution of the total transport in the current in a manner similar to the plotting of dynamic contour lines, by a very practical method developed by Ekman (1929, pp. 12–15).

With due consideration of all these advantages of the method, the simplified equation for the determination of volume transport given on page 29 will be used throughout for such estimates in this report.

So far we have only dealt with volume transport, but the method of considering only the two extreme stations also has an important application to the problem of velocities. From the same reasoning as that already used in the discussion of total volume transport, it is evident that the average velocity in any isobaric surface across the entire current is determined solely by the difference in dynamic height between the two extreme sides of the current and by its width, regardless of the distribution of velocities between. Since the dynamic height of the original and unmixed bodies of water between which the current has its existence as a contact phenomenon are determined solely by the static mass distributions within each body, the difference in dynamic height is not subject to influence by any dynamic forces, transverse or otherwise, and the enumerator of the equation for the average velocity across the entire current

$$v = \frac{h_1 - h_2}{2\omega \sin \varphi L}$$

is therefore rigidly fixed by the properties of the adjacent water masses. The uncertainty which attaches to the question of the average velocity therefore only applies to the quantity L in the denominator, or in other words to the distance over which the transition from one dynamic level to the other is spread. Since, under ideal circumstances, the flow of the current should be at right angles to this dynamic gradient between the two bodies of water, it is *ipso facto* obvious that the forces governing the variations of L must under the same circumstances be at right angles to the (resultant) gradient forces governing the propulsion of the current itself. An expression of the forces governing the magnitude of L, other than the deflecting force due to the earth's rotation, can consequently not be looked for in the velocities calculated by Bjerkness' equation. That is, since the assumption that the actual flow is at 90° to the dynamic gradient is based upon a consideration of the deflecting force alone as a transverse factor, other transverse forces added to the situation under natural conditions (see Parr, 1936 a, b, 1937 b, c) will necessarily alter this assumption, thereby also altering the mathematical relationship between dynamic gradient and current velocities, and another factor $f(x)$ must be added to the velocity equation.

$$v = \frac{h_1 - h_2}{2\omega \sin \varphi f(x) L}$$

On the other hand, the difference in mass properties between the adjacent bodies of water, as expressed in the difference in dynamic height between their surfaces, still remains an index to the total energy available for the propulsion of the current. The total mass transport must therefore remain unaffected by the forces $[f(x)]$ causing variations in L, the width or slope of the current. But the mass transport is also determined by the integrated sum of velocities across the current. Therefore, if for simplicity's sake we consider volume transport instead of mass transport, in a three-dimensional layer of infinitesimal thickness ΔD and therefore limited by parallel isobaric surfaces:

$$Vol.\ Tr. = \int \frac{\Delta h}{2\omega \sin\varphi f(x)\ \Delta L}\ \Delta D = \frac{h_1 - h_2}{2\omega \sin\varphi}\ \Delta D \qquad [1]$$

Since the term on the right is unaffected by the transverse forces $[f(x)]$ distorting the mathematical relationship between current velocities and dynamic gradient in the individual integrals, while the volume transport is also determined by:

$$Vol.\ Tr. = v.\ L.\ \Delta D$$

we therefore have:

$$v.\ L = \frac{h_1 - h_2}{2\omega \sin\varphi}$$

in which v stands for average velocity across the entire current and L for the total width. From this we see that the distorting effect of the transverse forces $[f(x)]$ must quite simply be automatically integrated in the quantity L. If this quantity is known, Bjerkness' velocity equation is therefore valid for the calculation of average velocities across the entire current, with only frictional dissipation of kinetic energy disregarded, while the same equation is not *a priori* valid for a computation of the distribution of velocities across the current unless one has adequate reason to assume the total absence of distorting transverse forces not taken into account in this equation.

In oceanographic philosophy Bjerkness' velocity equation may thus actually be regarded as a logical derivation of Ekman's principle of total mass transport determined solely by differences in mass distribution as expressed by differences in dynamic height, in spite of the fact that the latter principle developed historically as a derivation of the former. If, as an abstract example, we consider two bodies of different mass distributions and different dynamic heights, resting on a level bottom and separated by a rigid non-dimensional partition, Ekman's principle gives the potential mass transport which may take place between these two bodies of water after removal of the partition; while the velocity equation gives only a potentially infinite velocity in this situation. When the partition is removed a slope will develop between the two adjacent bodies of

[1] See page 29.

water, and the velocity equation simply determines the average velocity of the entire movement on the basis of the simple fact that the mass transport determined by the total difference in dynamic height regardless of slope is also the product of the average velocity and the cross section of the current which seems indicated after the slope has developed.[1] If the total cross section is accurately known, it is evident that the calculated average velocity must be correct. The velocity equation can thus only be applied to the empirically calculated slopes after their establishment, but, since it does not consider the various factors determining which of the infinite number of possible slopes between the two adjacent bodies of water will actually develop under natural conditions after withdrawal of the partition, it is evident that it does not provide a reliable means for calculating the distribution of velocities, as contrasted with the average velocity. The extent to which the velocity equation may be applied not only to the calculation of average velocity but also to the computation of the distribution of velocities is therefore dependent upon the assurance one may have of the insignificance of friction and the absence of acceleration and of transverse forces other than the deflecting force in any particular instance, but to proceed on the *a priori* assumption that these factors are generally without importance is patently very dangerous. Even when using the equation only to calculate total average velocity one must keep in mind that if special transverse forces are in operation the width of the actual current may possibly extend even into the regions of horizontal isobaric surfaces on either side of the calculated dynamic gradient, without affecting the total mass or volume transport, while changing the average velocity value.

Therefore, when the extreme boundaries of a current are empirically known, the calculated average velocity across its entire width, based upon the extreme stations only, may also under natural conditions be expected to show a good general agreement with the average velocities directly observed, while the same is not *a priori* true of the average velocities calculated for particular station intervals between. In the open ocean exact knowledge of the extreme boundaries of the current is not always easily obtainable, but when the flow is confined between rigid boundaries the question is greatly simplified and comparison can be made between two extreme sides of the channel itself. Under these circumstances the above considerations have found valuable application to the observations here reported upon, from which an excellent agreement is found between calculated and observed average velocities across the entire Straits of Florida, while very great discrepancies develop between calculated and observed distribution of velocities between the two sides of the Straits (see page 36).

[1] Or perhaps one should say, which must occur in replacement of the rigid partition if the two bodies continue to remain in dynamic equilibrium in their original lateral juxtaposition after the removal of the partition, without establishing a statically stable equilibrium by vertical superposition.

When transverse forces are in operation, the mass transport can of course also be calculated only for the entire current by the comparison of extreme stations alone as suggested on page 29, while the mass transport distribution is not capable of calculation in the same manner, being distorted in relation to the dynamic gradient in intermediate integrals in correspondence with the distortion of the velocity distribution above discussed. When Seiwell (1937, pp. 31–34) makes a calculation of variations in volume transport by a comparison between two stations both located on the *same side* of the main current, he actually applies the volume transport equation to the calculation of the distribution of volume transport (instead of only total transport) in separate current integrals in which his own observations of vertical oscillations demonstrate *the presence of transverse forces* not taken into account in the method of calculation he uses. When Seiwell further expresses the result in terms of percentage variation, instead of variation in absolute volume (see footnote 2, page 31), he therefore obtains a grossly exaggerated and meaningless expression of the relative significance of the variations in calculated volume transport (70.3%), while its actual and very much smaller relative significance (about 5%) could only be expressed by a comparison with a station on the opposite side of the main current.[1]

COMPARISON BETWEEN CALCULATED AND OBSERVED SURFACE VELOCITIES

At the anchor stations here reported upon, the surface velocities were sufficient throughout to be clearly recorded on a taff-rail propeller log designed for the use of sailing ships at slow speed, and the author is greatly indebted to N. C. Kelly, chief mate of the "Atlantis," for his ingenuity in arranging to have current observations made in this manner.

When comparing the surface velocities thus recorded from direct observations with those calculated from the hydrographic data by the use of the Bjerkness velocity equation, it is in this instance of great value to be able to make use of the principle already above developed (page 33) to the effect that while the average velocities thus calculated for the entire width of the gradient current may be expected to be valid in first approximation also under natural conditions, the same is not true of the particular velocities calculated for any subordinate fraction of the current width. In the case of the profile here discussed, we have an excellent example both of the approximate validity of the calculated total average speed and the apparent unreliability of the particular velocity calculations. In the accompanying figures 24 and 27 and table II, calculated and observed velocities are compared in detail.

[1] Compare with the variations and deviations from observed velocities shown by the surface velocities calculated for separate station intervals in table II, p. 37.

From this table it will be seen that the agreement between calculated and observed average velocities of the entire current is well within the limits of accuracy of a comparison of this sort. When an obviously reasonable interpolation from observed values of a velocity maximum between the first and second anchor stations is made, as indicated in figure 24, the fit is surprisingly good indeed, everything taken into consideration (the assumption of a stationary level at 600 meters, the nature of the instrument by which the current velocities have been recorded, etc.).

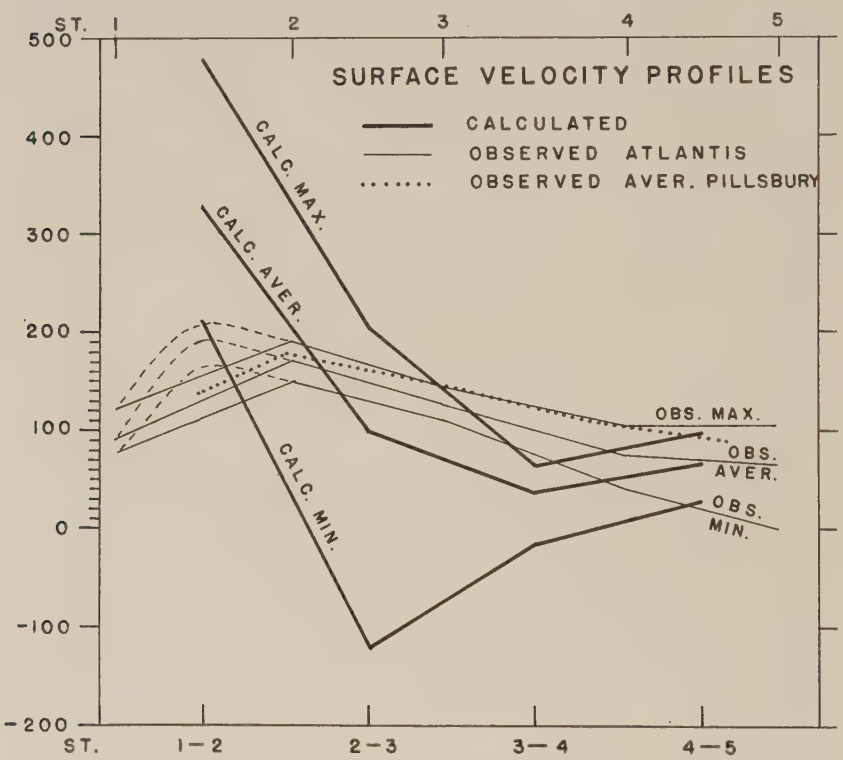


Figure 24. Comparison between calculated and observed surface velocity profiles. Dotted line for average velocities recorded by Pillsbury. Light solid lines for velocities observed by Kelly at Atlantis anchor stations.

A comparison with the recorded averages from direct current observations reported by Pillsbury gives an even closer fit between calculated and observed total average surface velocities of the entire current at this point, which may in part be due to the fact that Pillsbury's figures are averages for observations continued for a much longer period at each station (38–555 hours).

TABLE II. CALCULATED AND OBSERVED SURFACE VELOCITIES IN FLORIDA CURRENT

		Station 1	Stations 1–2	Station 2	Stations 2–3	Station 3	Stations 3–4	Station 4	Stations 4–5	Station 5
Observed	Max.	120		190		145		105		105
	Aver.	90		170		125		75		65
Cm.sec.	Min.	75		150		110		40		0
	Aver.[1]		130		147		100		70	
	Aver.[2]		160							
	Aver.[3]		141		178		125		92	
Calc.	Aver.		329		99		36		62	
	Aver.[4]		333							
Cm. sec.	Max.		481		208		64		98	
	Min.		212		−120		−17		29	
Calc. Aver. vel.			254[1]		67[1]		36[1]		88[1]	
% of obs. aver.			206[5]							
velocities			236[6]		56[6]		29[6]		67[6]	

Average deviations: 66% of obs. vel.[1] or 54% of obs. vel.[5] or 96% of obs. vel.[6]

Average observed velocities entire current 112 cm. sec. 120 cm. sec.[5]
Average observed velocities entire current according to Pillsbury 136.5 cm. sec.[5]
Average calculated velocities:
Direct calc. St. 1–St. 5 133 cm. sec. = 118.5%[1] or 110.5%[5] of simultaneously obs. aver. or 97% of av. obs. by Pillsbury
From table above: 136 cm. sec. = 121%[1] or 113 %[5] of simultaneously obs. aver. or 100% of av. obs. by Pillsbury

[1] Rectilinear interpolation of velocities between St. 1 and St. 2.
[2] Freehand interpolation to maximum velocity between St. 1 and St. 2. See text.
[3] By rectilinear interpolation from average velocities recorded by Pillsbury.
[4] Assuming constant dynamic height 300–600 decibars at St. 1. See text.
[5] Using interpolated maximum velocity between St. 1 and St. 2. See footnote 2.
[6] Using average velocities recorded by Pillsbury (footnote 3).

From figure 27 it will finally be seen that we have a complete record of direct velocity observations for all stations for lunar hours 8 to about 14. If the observed average velocities for lunar hours 9 and 12 are calculated from the station velocity curves, we again find a very good agreement between calculated and observed average velocities for the entire current also for these particular lunar hours (see table III) especially when the comparison is made with calculations based upon the assumption of a variable dynamic height of the 300 decibar surface relative to the 600 decibar surface at st. *1*.

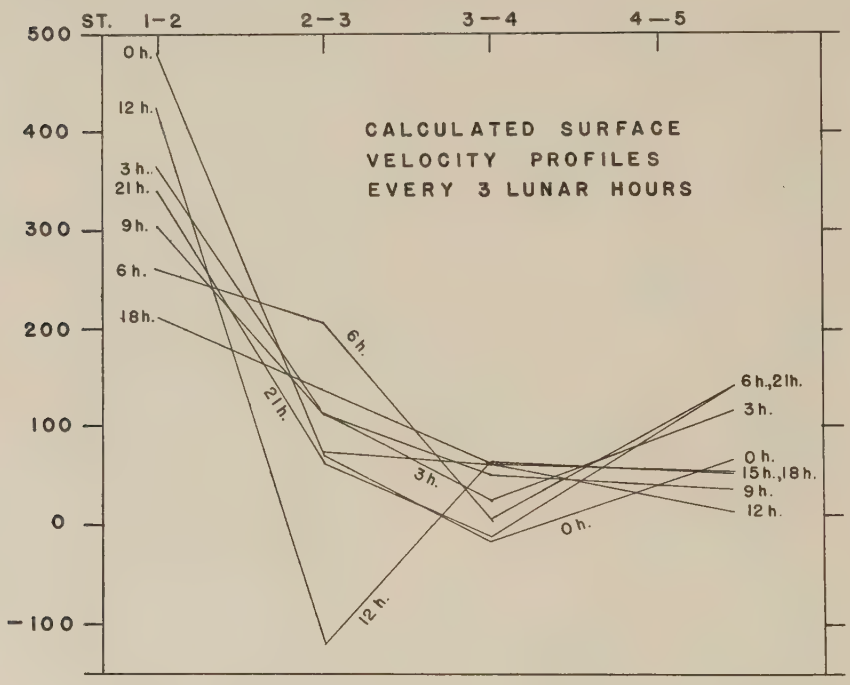


Figure 25. Calculated surface velocity profiles for every 3 lunar hours.

At the same time as the data thus fully confirm the thesis that the Bjerkness equation may generally be valid for calculations of average velocities for the entire current, they also give an excellent illustration of the statement that this is not necessarily true of the calculations for any particular fraction of the current ribbon, by showing an average discrepancy for individual station intervals of one-half to two-thirds of the observed velocities, and in comparison with the average velocities recorded by Pillsbury those calculated from the "Atlantis" observations give a mean deviation of nearly 100 per cent for individual station intervals.

This indirectly also confirms the superior value of volume transport estimates made directly from the end stations only, as compared with estimates based upon the distribution of volume transport in intermediate station intervals (see page 29).

To decide whether the discrepancies developing in individual station intervals might possibly be due only to errors of observation, calculations were made of the average slope required to give by computation the distribution of velocity shown by the average velocities observed at each station. For this purpose the calculations were started on the basis of the average dynamic height of the surface relative to 600 decibars computed for anchor station *4*, where the spread between maximum and minimum calculated heights is the least; and the velocity maximum interpolated from observations between the first and second stations

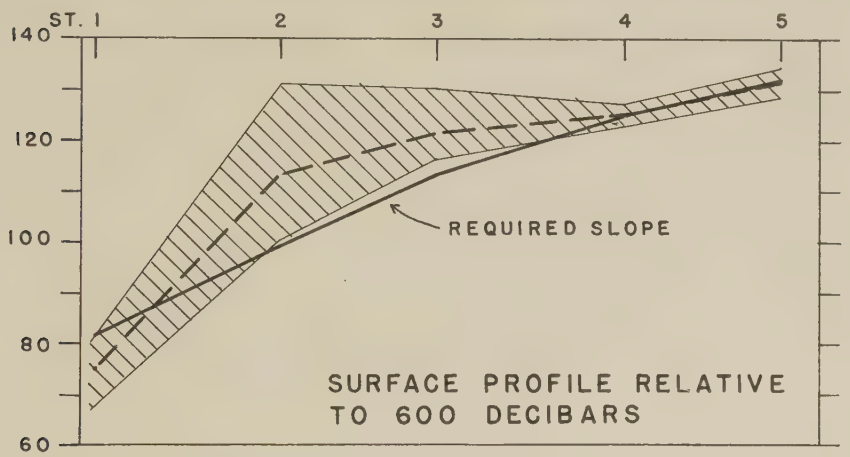


Figure 26. Comparison between relative dynamic slope of the free surface required for average observed velocity distribution according to Bjerkness' equation and range of variations in dynamic slope (hatched) calculated from hydrographic observations (average in broken line).

was used to calculate the dynamic height required at station *1*. In figure 26 the average dynamic slope required to give the observed velocity distribution is compared with the ranges of variations in dynamic elevations calculated from the hydrographic observations at each station. From this figure it will be seen that not only would individual observations have to be grossly erroneous in fact, but every single series made at the first three anchor stations, 36 series altogether, would have to include a significant gross error, since even the total ranges of variations in calculated dynamic height at these stations fall outside of the required average. The data, and all laws of probability, give absolutely no reason for assuming such universal errors in every one of these 36 series, particularly not when we notice that there is at the same time a very good agreement be-

tween required average slope and that calculated from the 24 series made at the fourth and the fifth anchor stations.

If the variations in point of time in calculated velocities for each station interval and in the average velocities[1] for the entire series are tabulated and compared with the averages of maximum and of minimum velocities recorded

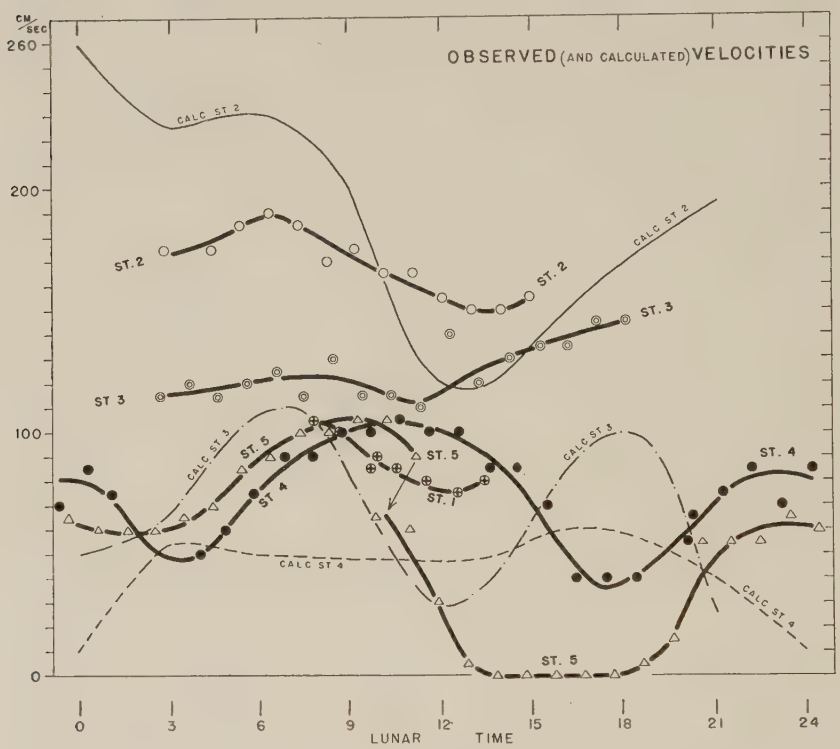


Figure 27. Comparison of variations in surface velocities observed by Kelly at anchor stations 1–5 (heavy lines) with curves interpolated from calculated velocities (lighter lines).

by the taffrail log, as done in the accompanying table III,[2] we again find very good agreement with regard to maximum velocities and a fair agreement with regard to minimum velocities.

[1] The computation of average velocities from hydrographic conditions at the end stations only and by integration of calculations for all station intervals give exactly the same values, in accordance with expectations, as shown in the table.

[2] The available records of observed velocities are unfortunately only fractional for the first 3 stations, particularly for station *1*.

In fig. 27 the observed velocity curves at the five stations are further compared with the velocities interpolated from the calculated velocities of the adjacent station intervals. From this comparison several interesting points may be noted. Firstly, there seems to be an inverse relationship between the amplitude of variations in calculated and observed velocities. The greatest

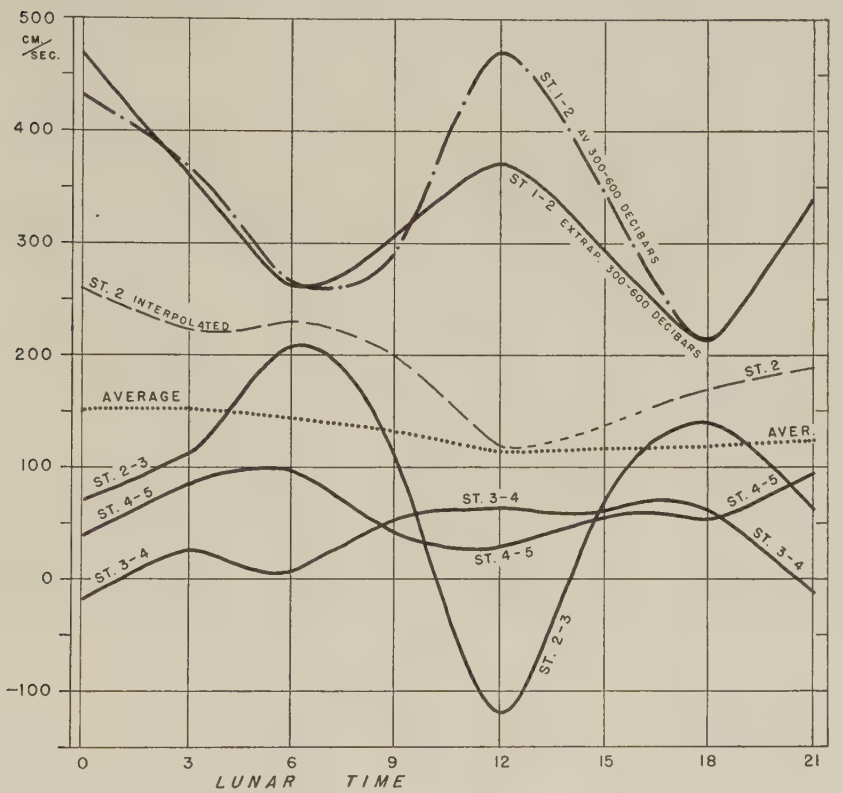


Figure 28. Variations in calculated surface velocities in all station intervals, and in average velocity of entire profile. Velocities in first station interval calculated on the basis of a constant elevation of the 300 decibar surface relative to 600 decibars drawn in dot and dash; velocities calculated with variable extrapolated values (see text) in solid line.

amplitudes of calculated velocities are obtained for stations *2* and *3*, with comparatively slight amplitude for station *4;* while in the observed velocities the amplitudes of variations at stations *4* and *5* are much greater than at stations *1–3*. Secondly, we notice a quite good agreement with regard to phase between calculated and observed velocities at stations *2* and *3*, while there is an inversion of phase at station *4*. If we now compare fig. 27 with fig. 28, in which the

TABLE III. VARIATIONS IN CALCULATED VELOCITIES IN POINT OF LUNAR TIME

Lunar Time		$\frac{0}{24}$	3	6	9	Moon's transit 12	15	18	21
Calculated Velocities Cm. sec.	St. 1–2[1]	481	363	261	307	422		212	340
	St. 1–2[2]	431	367	264	290	481		213	334
	St. 2–3	71	113	208	112	−120	72	140	63
	St. 3–4	−17	25	7	51	64	60	62	−13
	St. 4–5	40	87	98	40	23	55	54	94
Calculated Averages Cm. sec.[1]		151.0	150.8	141.9	131.8	110.6		118.7	124.3
From table above[2]		137.4	151.9	142.7	127.2	126.6		119.0	122.7
Dir. est.[1]		150.7	150.7	141.8	131.9	110.4		118.7	124.3
St. 1–5[2]		137.3	151.9	142.7	127.1	126.5		118.9	122.7
Average observed vel.:					124.4	106.0			

Average of observed maximum velocities:
138 cm. sec. by rectilinear interp. St. 1–2. 145 cm. sec. by interp. of max. betw. St. 1 and St. 2.
Maximum calculated average velocity, identical lunar time 152 cm. sec.
Maximum calculated average velocity, regardless of lunar time 157 cm. sec.
Average of observed minimum velocities:
82 cm. sec. by rectilinear interp. St. 1–2. 90 cm. sec. by interp. of max. betw. St. 1 and St. 2.
Minimum calculated average velocity, identical lunar time 110 cm. sec.
Minimum calculated average velocity, regardless of lunar time 110 cm. sec.

[1] Using variable values of dynamic height of 300 decibars relative to 600 decibars extrapolated per Station I. See text.
[2] Using average of extrapolated dynamic heights of 300 decibars relative to 600 decibars at Station I. See text.

calculated velocities are plotted according to station intervals instead of according to stations, we see that an interpolation of observed velocities in the first station interval (st. *1–2*, fig. 28) from the recorded velocities at these two stations (fig. 27) would give maximum observed velocity around lunar hour 6 and minimum observed velocity around lunar hour 12, which represents a complete inversion of phase from that of the calculated velocity curve (fig. 28). If we make a similar interpolation from the velocity curves for stations *4* and *5* in fig. 27 and compare with the calculated curve for station interval *4–5* in fig. 28, we again obtain fair general agreement, but with the observed velocity curves lagging about three hours behind the calculated curve. The significance of these variations in the relationship between observed and calculated velocity curves is not very clear, but the inversion of phase in this comparison at the left side of the current proves beyond any doubt that the forces responsible for the observed changes in dynamic height, particularly at station *2*, are not directly related to longitudinal velocities, but must express themselves in transverse movements at right angles to the main direction of the current.

Comparison with the time distribution of the velocities recorded by Pillsbury gives very poor agreement throughout, even to the extent of an indication of opposite phases at identical lunar times. Further difficulties in this comparison arise from the fact that Pillsbury's observations at station *1b* (Pillsbury 1886, 1887) show changes in the phase of the surface current velocity curve in relation to lunar time from minimum to maximum velocities at the time of the moon's transit during the several days of continued observations in this location. With hydrographic observations only available for a period of 24 hours, a further discussion of the relationship of this recorded change in phase to changes in hydrographic conditions would scarcely prove very profitable at this time, and the analysis of the problem involved must be left for future research.

VOLUME TRANSPORT

Table IV shows the calculations of volume transport directly from the end stations, and the results are plotted in figure 29. It will be noticed that while the assumption that the variations in dynamic height of the 300 decibar surface relative to 600 decibars at station *1* obtained by rectilinear extrapolations from the rest of the profile (fig. 22 and p. 25) gives a vastly increased range of variation for calculated volume transport of the entire current, the 24-hour averages on the other hand are approximately identical whether calculated on this assumption or on the assumption of a constant dynamic height of the 300 decibar surfaces relative to 600 decibars at station *1*, corresponding to the average of the extrapolated values. Using the latter values, we obtain 24,984,000 m^3 per sec., while the variable values give 25,207,000 m^3 per sec. as the average for a full lunar day. This is in accordance with the fact that the increased range of variations in volume transport calculated with variable height of the 300 deci-

TABLE IV. VARIATIONS IN CALCULATED VOLUME TRANSPORT

Lunar Time		0/24	3	6	9	Moon's transit 12	15	18	21	X 25 Decibars
St. 1 Dyn. h. rel. 300 decibars	0 Decib.	54.4	49.5	54.8	55.7	55.3	(57.0)	60.0	60.2	× 1
	50 Decib.	35.4	31.8	36.6	37.2	37.0	(38.4)	40.5	40.5	× 2
	100 Decib.	20.5	20.0	22.3	22.0	22.3	(22.7)	23.6	24.8	× 2
	150 Decib.	13.1	13.3	15.0	13.8	14.4	(14.5)	14.1	14.9	× 2
	200 Decib.	8.1	8.3	9.3	8.7	9.0	(9.0)	8.8	9.0	× 3
Dyn. h. 300–600 decibars	[1]Extrap.	13.5	19.7	19.6	17.2	26.0	19.8	19.3	18.5	×(8+10)
	[2]Aver.	19.2	19.2	19.2	19.2	19.2	19.2	19.2	19.2	×(8+10)
Average Dyn. height[1] 0–600 decibars[2]		19.154	23.300	24.304	22.392	29.071	24.650	24.592	24.192	
		23.429	22.925	24.004	23.892	23.971	24.307	24.462	24.728	
St. 5 Dyn. h. rel. 600 decibars	0 Decib.	131.8	133.1	134.6	128.8	128.2	129.5	129.7	131.5	× 2
	100 Decib.	92.0	92.3	92.6	90.2	89.6	90.3	91.4	91.7	× 3
	150 Decib.	74.8	74.2	75.0	73.2	73.7	75.0	75.0	74.7	× 2
	200 Decib.	61.9	61.3	62.3	61.7	61.9	62.5	62.5	61.7	× 3
	300 Decib.	43.5	43.1	42.9	43.5	43.5	43.9	43.7	43.7	× 4
	400 Decib.	27.4	27.2	26.8	27.2	27.3	27.4	27.3	26.7	× 4
	500 Decib.	12.9	13.0	12.8	12.7	12.7	12.7	12.7	12.2	× 4
Av. Dyn. h. 0–600 Db.		50.421	50.358	50.579	49.721	49.679	50.142	50.246	50.125	
$h_5 - h_1$ Dyn. cm.[1]		31.627	27.058	26.275	27.329	20.608	25.492	25.654	25.933	
2		26.992	27.433	26.575	25.829	25.708	25.942	25.729	25.408	
Volume transport[1] 1000 m.[3] pr. sec.[2]		30,156	25,800	25,054	26,059	19,650	24,307	24,462	24,728	
		25,737	26,158	25,340	24,628	24,513	24,736	24,533	24,227	

[1] Using extrapolated variable dynamic height of 300 decibar surface relative to 600 decibars at Station 1.
[2] Assuming constant average dynamic elevation of 300 decibar surface relative to 600 decibars at Station 1.

bar surface relative to 600 decibars at station *1* is mathematically due solely to these extrapolated variations.

Since it would be patently unreasonable on the basis of the variations in the hydrographic profiles shown in fig. 22, p. 25, to assume a constant elevation of 300 decibars relative to 600 decibars at station *1*, and since the variations must obviously be in the direction of the extrapolated variations, the true curve for diurnal variations in volume transport must be somewhere between those calculated in the table, although it is by no means entirely excluded that its range may even exceed the range shown by the use of the individual extrapolated values for the elevation of the 300 decibar surface relative to 600 decibars, instead of their average. The rectilinearly interpolated average of the two curves is also indicated in fig. 29.

On this point it becomes of interest to evaluate variations in volume transport potentiality of the two extreme stations separately by the method already discussed on page 31. At st. *5* the extreme range of variations in average dynamic elevation relative to 600 decibars is 49.679–50.579 dyn. cm. which gives

$$Var.\ Vol.\ Tr._{st.\ 5} = \frac{0.9}{2\omega \sin \varphi}\ 600 \times 10^4 = 858{,}000\ \text{m.}^3\ \text{pr. sec.}$$

For station *1* we get, when using variable extrapolated elevations of the 300 decibar surface relative to 600 decibars, a range of variations of 19.154–29.071 dyn. cm., giving:

$$Var._1\ Vol.\ Tr._{st.\ 1} = \frac{9.92}{2\omega \sin \varphi}\ 600 \times 10^4 = 9{,}463{,}000\ \text{m.}^3\ \text{pr. sec.}$$

If we consider only the observed variations at station *1* relative to 300 decibars for the determination of $h_1 - h_2$, (which is the identical procedure as that of considering the elevation of 300 decibars relative to 600 decibars to be constant) we get a range of 17.050–20.633 dyn. cm. giving:

$$Var._2\ Vol.\ Tr._{st.\ 1} = \frac{3.58}{2\omega \sin \varphi}\ 300 \times 10^4 = 1{,}707{,}000\ \text{m.}^3\ \text{pr. sec.}$$

Variations within the observed depths at station *1* alone, where absolutely no suspicious irregularities are noticed in the data, thus account for at least a minimum diurnal variation of 1.7 million m.^{3} sec., while st. *5* accounts for at least 800,000 m.^{3} sec. The variations at the two stations are potentially cumulative, and might appear entirely cumulative by a study of observations taken at random in point of time, but by the synchronization with reference to lunar hours used in tables III and IV (bottom line) only a maximum of 1.9 millions of the potential 2.5 million m.^{3} sec. variation seems realized.

If the variations in relative dynamic height of the 300 decibar surface relative to 600 decibars at station *1* are actually as great as assumed from the variable extrapolated values used in table IV, and in the computation of *Var., Vol. Tr.*$_{st.1}$, above, a total variation of over 10 million m.^{3} sec. would be possible, and this as one will notice is realized to the full even when the data are synchronized with reference to lunar time.

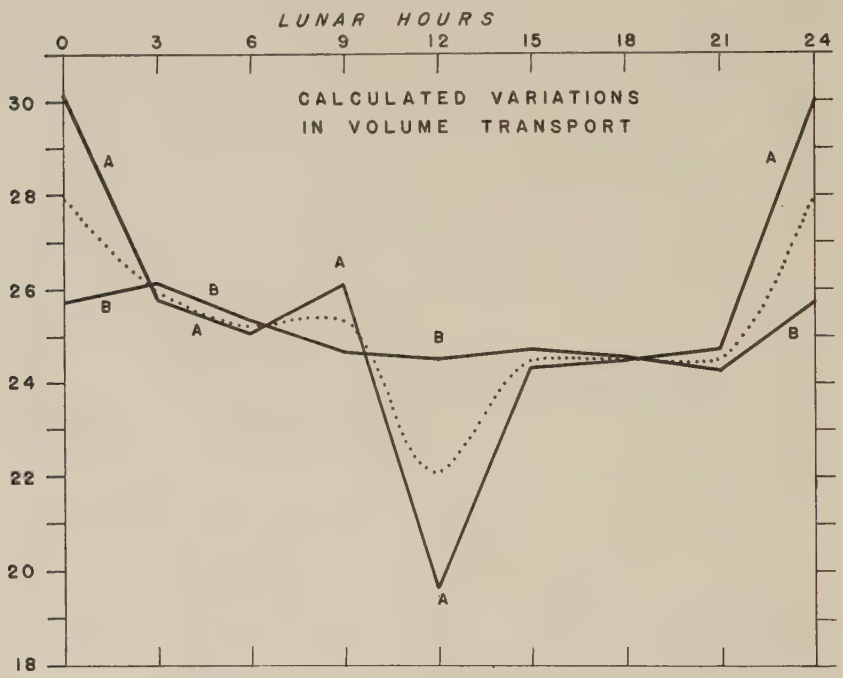


Figure 29. Variations in total volume transport in million cubic meters per second (scale at left). Curve A calculated on the basis of extrapolated variable dynamic height of the 300 decibar surface relative to 600 decibars at Station 1; curve B on the basis of a constant relative elevation. Dotted line represents arithmetic mean of curves A and B.

It will be noticed that the 24 hour average volume transport above calculated is in amazingly good agreement with the volume transport calculated by Wüst from "Bache" observations in the same profile as the anchor stations here reported upon (Fowey Rocks—Gun Key). Wüst (1924, table II, p. 42) gives 25.55 million cubic meters per second as compared with 24.98–25.21 million m.^{3} sec. calculated from the present data.

In the case of our own series, however, it is important to note that the calculations have only been made between extreme stations, without extrapolations to shore. Since both extreme stations are in regions of outward flow, an addition

to the volume transport must be made by extrapolation. By rough evaluation this addition might amount to about 5–8 million m.^{3} sec. bringing the total transport to somewhat more than 30 million m.^{3} sec. It is not quite clear from Wüst's account whether such extrapolations are included in his figures or not.

These figures can also be compared with volume transport calculations for the Caribbean and Cayman seas. For the purposes of such comparisons, the profiles indicated in figure 30 have been calculated from the hydrographic conditions at their end stations.

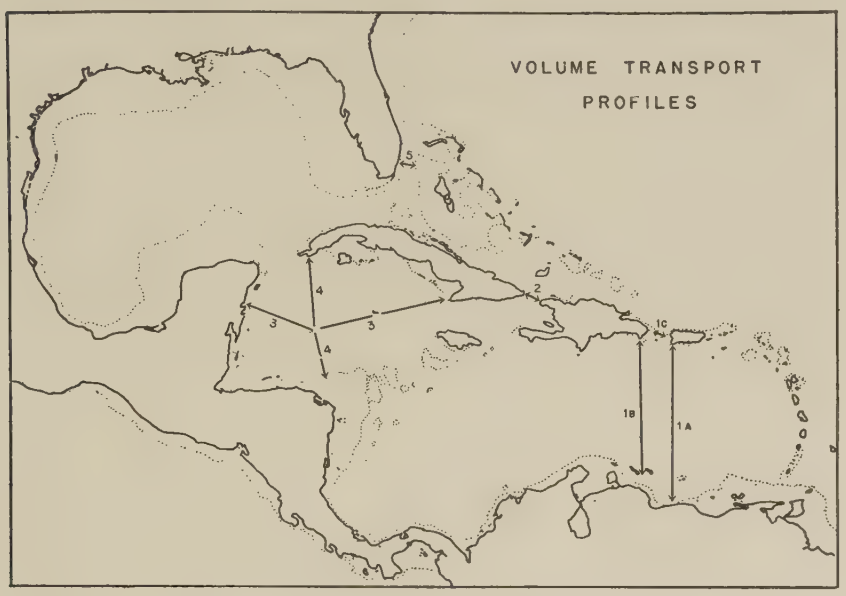


Figure 30. Locations of profiles used for volume transport comparisons.

Profile 1A is based upon an "Atlantis" series from 1937, extending from shore to shore across the Caribbean, and it gives 29.46 million m.^{3} pr. sec. The calculation of 1B, "Atlantis" 1933, is shown in table I on page 30, and gives 37.13 million m.^{3} pr. sec., but in this profile, which does not extend to shore, a counter current is indicated in the most southern station interval. If this counter current extended to the shore at that time, it would require a deduction of about 7 million m.^{3} pr. sec., bringing the total of profile 1B into agreement with that for 1A at about 30 million m.^{3} pr. sec. The Mona Passage, profile 1C, "Atlantis" 1933, is only calculated to contribute about 70,000 m.^{3} pr. sec., which is insignificant in this comparison between profiles 1A and 1B.

Profile 3, "Atlantis" 1933, stretches across the Cayman Sea from east to west and gives a net volume transport to the north of 31.92 million m.^{3} pr. sec.;

and profile 4, representing a combination of a 1934 and a 1933 end station, gives 33.92 million m.^{3} pr. sec. going to the westward from where it can only escape to the north.

Four different profiles across the wider portions of the Caribbean and Cayman seas thus agree remarkably well in showing a net volume transport through this region of 30–34 million cubic meters pr. sec., which in turn agrees with the calculated 24-hour average outflow through the Straits of Florida (extrapolated marginal flow included). And since furthermore the average calculated velocities in the Straits of Florida agree with the average observed velocities at the surface, and in Wüst's data also show a good agreement between entire calculated and observed velocity profiles, it seems fairly safe to set the entire net transport for the Central American basins at this value of 30–34 million cubic meters per second.

It should be mentioned, however, that the calculations break down completely when applied to various of the narrower passages. Thus the Yucatan Channel calculations give too low values (18–29 million m.^{3} pr. sec.), and the data for Windward Passage (profile 2, "Atlantis," 1933) would indicate an inflow of about 13 million m.^{3} pr. sec., which is not accounted for in the outflow. These difficulties will be taken up for fuller discussion in a subsequent report on the quantitative dynamics of the Central American seas, but until a solution has been found they must always remain a source of some uncertainty with regard to all calculations for this region.

TRANSVERSE MOVEMENTS

When first plotting the time profile for station *2*, the author felt rather in despair of the possibility of such a situation as that shown by the series *J*. But in drawing the space profile for the corresponding lunar hour 3 (fig. 12) from a combination of the time profiles for all stations, he was both surprised and relieved by discovering that the peculiar observations of this series might indeed form a quite logical combination with the conditions observed at the same lunar hour at station *1*, and at the other stations, the picture showing a body of water of comparatively high salinities to the left of the main current, separated off from similar high salinities to the right. When the succession through the other profiles shown in figs. 12 and 13 is studied further, it will be seen that they may indeed be interpreted to indicate an extrusion and occlusion of water to the left occurring twice during the lunar day. For this interpretation it is only necessary to assume that the extrusion still observable at lunar hour 21 has passed with the current beyond the line of observation by the time of its occlusion at lunar hour 0 or 24. A diagrammatic series of illustrations of such a possible progression with reference to line of observation is shown below the series of profiles (figs. 12 and 13, p. 14–17).

This picture might be considered very disturbing if it were not for the fact

that Rossby's wake stream theory of ocean currents, based upon theoretical as well as experimental research, does require the periodic occurrence of such extrusions from the main current to the left (Rossby, 1936). Perhaps therefore, by good fortune, the anchor station observations of the "Atlantis" in the Straits of Florida happened to be made at a time at which such extrusions were being formed in the proximity of the line of observations.

If we now plot a time-space projection of the distribution of maximum salinities through our profile, the geometrically simplest picture which can be drawn is that shown in fig. 31. In this picture it will be noticed that the extrusion shown at the right can be combined with the extrusion on the left side of the illustration to form the tail end of the latter; giving only one maximum, or completed, extrusion recorded at the line of observations around lunar hour 15 (possibly combining the effects of two minor impulses recorded around lunar hours 15 and 21), and one or two minor or aborted extrusions recorded around lunar hours 3 and 9.

This geometrically simplest interpretation, however, seems logically the least sound one, since it does not take into account the distortion of the picture which must result from the effects of the transverse velocity gradient. Indeed it is entirely contrary to the distortion to be expected, in that it shows the arrival of the left end of the extrusion at the line of observations earlier than the arrival of the central portions, in spite of the fact that the current velocities at the left are unquestionably lower than at the center.

According to the vertical velocity curves given by Pillsbury (1886, 1887) from direct observations, the movement of the maximum salinity layer in the depth at which it was observed at the "Atlantis" stations should on the average be fastest at anchor station *3* and slowest at anchor station *1*, with intermediate and almost identical velocities at stations *2* and *4*. (Since Bjerkness' velocity equation is not applicable to the calculation of the distribution of velocities from the calculated dynamic gradients in the case here reported upon (see p. 38), we can only refer to Pillsbury's observations for approximate information of the velocity distribution at deeper levels.)

If the transverse impulse of extrusion originates at some distance upstream, the left side of the extrusion should therefore be expected to lag behind the corresponding right portions by the time of their arrival at the line of observation. Fig. 31 can accordingly also be drawn as shown in fig. 32, without violation of any of the data of direct observation. In this latter figure we find two completed extrusions in the course of a lunar day, and if the course of the 36.2 isohaline is taken as an index of the periodicity, the extrusions occur exactly on a 12 lunar hour period. However, variations in the transverse velocity gradient, and the apparent superimposition of a diurnal period, as shown by the 36.1 isohaline upon the semi-diurnal period, will also introduce a distortion in the periodicity shown by individual isohalines in an illustration of the kind shown in fig. 32, so that the identical periodicities cannot be expected to be

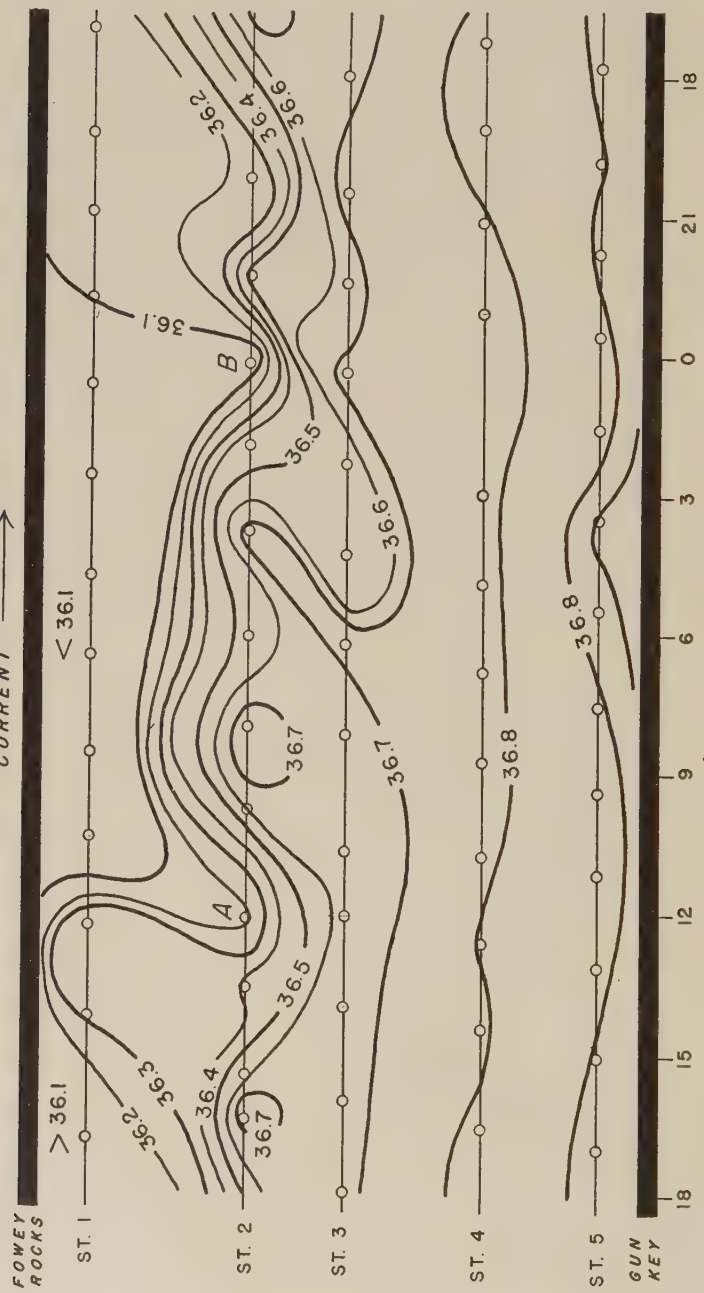


Figure 31. Time-space distribution of maximum salinities regardless of depth. Geometrically simplest presentation. Total width about 80 kilometers.

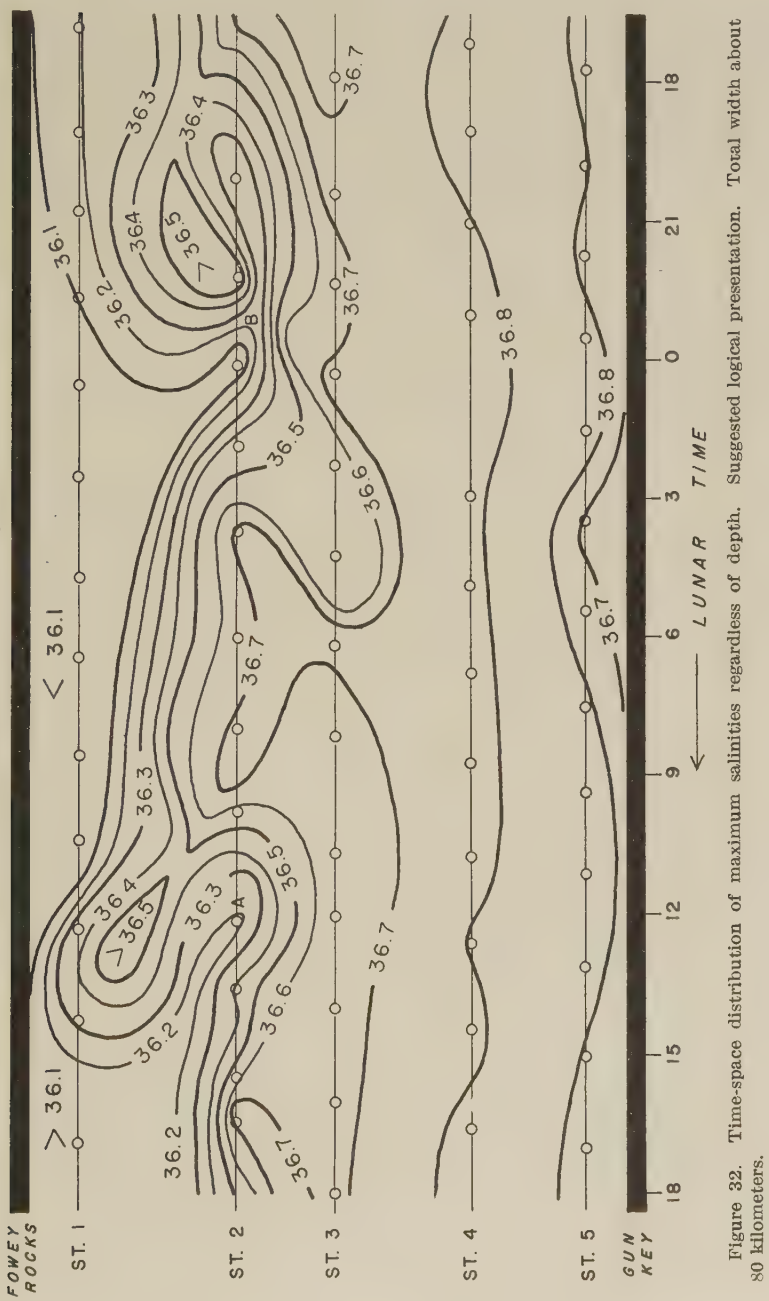


Figure 32. Time-space distribution of maximum salinities regardless of depth. Suggested logical presentation. Total width about 80 kilometers.

indicated in all the individual isohalines. However, a predominant semi-diurnal periodicity of extrusions seems indicated in a general way. The diagrammatic illustrations at the bottom of figs. 12–13 are based upon this assumption.

With regard to the peculiar distribution of the 36.7 isohaline between stations *2* and *3*, this may possibly have its origin in the fact that while the average velocities as recorded by Pillsbury are higher in the maximum salinity layer at station *3*, the velocities at both stations are so extremely variable that if the extrusion of the 36.7‰ water to the left should occur at the period of minimum velocities in the longitudinal zone of station *3* and maximum velocities in the longitudinal zone of station *2*, this extruded body might become greatly extended longitudinally in the zone of station *2;* and after the velocity gradient between the two zones has again reversed itself to the normal relationship, this extension in zone *2* might appear as an extension in both directions, upstream and downstream.

According to Rossby, the extrusions to the left should occur periodically as the lateral stresses due to the development of the transverse velocity gradient accumulate to a certain maximum. While the extrusions would thus have a periodicity of their own even in the absence of other variable forces than that of the lateral stress, it is, on the other hand, quite logical to assume that in the presence of other variable forces of a more definite periodicity, this periodicity might be impressed upon the time pattern of the lateral extrusions. That is to say, with variable tidal forces in operation it would be a highly unlikely assumption that each stage in the variations of these forces should be absolutely equally favorable or unfavorable for the release of a lateral extrusion. If, on the contrary, the more reasonable assumption is correct, that a certain state of the tidal energies may be more favorable, other states less favorable for such extrusions to occur, then the periodicity of these tidal forces should patently be expected to tend to gain control over the periodicity of the lateral extrusion, and our interpretation of the anchor station observations indicates that this may possibly be true, with the semi-diurnal lunar period predominant.

While the potential energy magnitude of the direct lunar influences are of course very slight,[1] the tidal forces indirectly derived from lunar influences are patently very great in the profile here considered as shown by the diurnal and

[1] It might be mentioned at this point that since the effect upon pressures of the gravitational force is in proportion to the mass, and since the greatest densities on the northern hemisphere always occur at the left side of the current, the effect of the moon's attractions and of the earth-moon rotation will always tend to reduce the transverse pressure gradient from left to right. While the difference in itself is almost infinitesimal, and could not directly provide a change in energy distribution sufficient to explain any transverse movements, it is not inconceivable that this extremely slight difference might have some cumulative effects possibly setting in motion greater forces by upsetting their normal equilibrium.

semi-diurnal variations in the surface velocity observations of the "Atlantis" (fig. 27, p. 40) and in the velocities at all depths observed by Pillsbury (1886, 1887). Since, according to Rossby, it is the development of the transverse velocity gradient which creates the extrusions, it is evident that tidal forces capable of causing velocities to vary by 25 to more than 100 per cent of their average value, at all depths of significant current speeds, must exercise a profound influence upon any transverse movement caused by variations in the transverse velocity gradient, and must tend to gain control over the periodicity of these movements.

With regard to the locations in which the extrusions are likely to occur, there is *a priori*, particularly in currents of variable velocities, no reason at all to assume that the location remains stationary. On the contrary, this would be an assumption of a singularity out of an infinite number of equal possibilities. The fact that the Bache observations as calculated by Wüst (1924) show such excellent agreement with Pillsbury's current observations, in contrast to the disagreement between calculated and observed velocity distributions in the "Atlantis" series, may be fortuitous or may indicate that similar extrusions were not in the process of formation in this region either at the time of the "Bache" observations or when Pillsbury made his records.

It should be mentioned at this point that the requirements for the formation of such extrusions is based upon the development of the relative velocity gradient stresses *in the water*, and it is not necessarily required that the extruded body becomes immediately included in a counter current *relative to the surface of the earth* (see Rossby, 1937). It is therefore not suggested that the extrusions herein discussed must be carried back into the Gulf of Mexico or the Caribbean. On the contrary, they are assumed to be moving out of the Straits of Florida only at the lower velocities obtaining on the left side of the current.

While the entire extrusion is thus flowing outward, it is evident that it must be associated with an eddy formation in terms of relative velocities within the moving water, that is to say, it represents a marginal eddy moving with the entire current system. This relative eddy motion must lead to an inversion of the posterior part of the outer boundary of the extrusion, ultimately bringing it into contract with its own continuation as the normal boundary of the current ribbon from which it was originally extruded. When this contact is established, a reabsorption from right to left should begin to take place, completing the cycle required by Rossby's interpretation of the relationship between main relative current and the relative counter current on its left. If another series of anchor stations had been made simultaneously farther downstream (to the north) one might have had opportunity to get a picture also of this second phase of the phenomenon; but even our fig. 32 indicates fairly clearly the beginning of this return movement and reabsorption at least in the case of the first extrusion shown at the right.

Finally, it might be pointed out that in accordance with expectations (Parr,

1936 b; Rossby 1936) the transverse movements follow approximately along the isopycnal surfaces and entirely within the range of the pycnocline (σ_t 24.5–26.5), as shown by the course of the isopycnal zone for σ_t 25 to σ_t 26 indicated by hatchings in every second profile illustrated in figs. 12–13.

It should be kept in mind also that the observations at the five anchor stations were not made simultaneously but on succeeding days; and if the extrusions are of a semi-diurnal periodicity the combination of the records from the various stations is an artificial combination of observations of entirely separate extrusions, justified to the extent that the semi-diurnal period predominates over variations of longer periodicity, but erroneous to the extent that such variations over a longer period may have found expression during the somewhat less than six days taken by the entire series of observations. This difficulty, however, there is absolutely no way of avoiding.

In a report just published, Seiwell (1937) has subjected a series of observations made over a five-day period in the open Atlantic to a study of vertical oscillation in which he comes to the conclusion (loc. cit. p. 17) that "it is reasonable to conclude that vertical oscillations of temperature (and other properties of sea-water) in the locality represented by station 2639 resulted primarily from vertical oscillations of the water column rather than from horizontal displacement of the water layers." With this conclusion the present writer is inclined to disagree, at least to the extent that he cannot recognize that Seiwell's data give any more evidence of vertical than of horizontal movement. Seiwell arrived at his conclusion from a consideration of the extent to which the entire ocean would have to move around horizontally to produce the vertical variations observed at his station, on the assumption that the slopes of the internal boundaries would remain constant in the course of such a process; in other words, with the ocean moving as a rigid body and not as a liquid. Logically this assumption implies that horizontal translation, that is, lateral extrusion and intrusion, can occur without vertical distortion of internal boundaries; and that vertical oscillations can take place without horizontal variations of motion so as to produce the observed elevations or depressions. Either implication is of course impossible, and unquestionably entirely unintended.

In fig. 33 the effect of the entrance of a lateral intrusion through our first station vertical *A* is diagrammatically illustrated, on the assumption that the intrusion enters between originally horizontal upper boundary at height *A* ($H_A = H_B$) and a rigid lower boundary at height *O*. At station *A* we will then observe an elevation of the upper boundary of the magnitude ΔH. If a similar elevation has not yet occurred at station *B*, or if we have no evidence to show whether it has occurred or not as in the comparisons made by Seiwell, we are limited to the assumption that the intrusion has not yet reached to station vertical *B*. At the time of the observation of the increased height of the boundary (H_{A2}) at st. *A*, the profile of the liquid boundary between st. *A* and st. *B* may have different forms such as those indicated by the curves 1–3 in the figure.

For simplicity's sake we assume that the area included between the new and old boundary profile between st. A and st. B is simply in the form of a triangle $H_A\ H_{A2}\ H_B$, and all we have to account for is the invasion of the volume of water occupying this triangle.

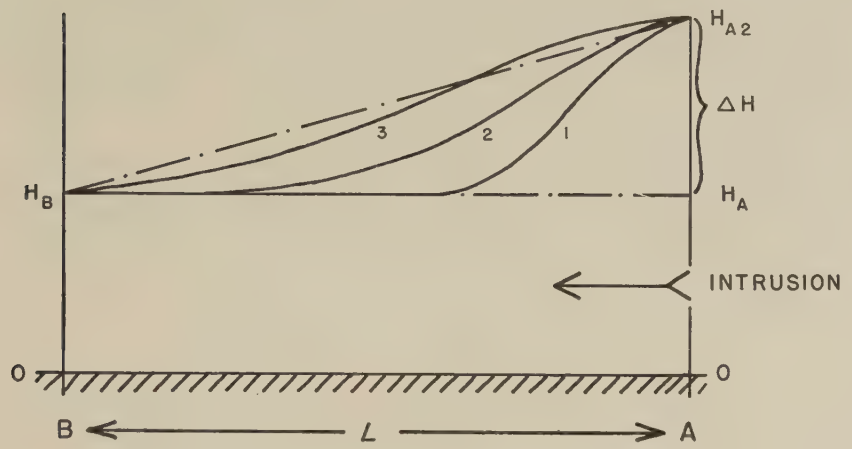


Figure 33. Effect of an intrusion upon a flexible boundary surface.

It may now be noticed that this volume invasion must be accounted for in equal degree whether we assume with Seiwell that it is reversible, and therefore to be designated as a vertical oscillation only, or whether we assume it to be a progressive intrusion representing a horizontal displacement, expressed simply by a lateral acceleration of the entire layer involved. A comparison made on the basis of volume transport and required velocities is therefore entirely inconclusive and not pertinent to the problem of whether we are dealing with vertical oscillations, only, or with progressive horizontal displacements, since the same values must be explained by either interpretation.

It is nevertheless of interest to give some further consideration to Seiwell's data. Since in this case we are not dealing with a rigid lower boundary, we must consider the variations in area between two variable boundaries, and for this purpose we will use the isothermal surfaces of 10° C and 17° C, which have also been selected by Seiwell for particular consideration (*loc. cit.*, p. 17). Since we are dealing with only one station and do not have a fixed station distance L, as between A and B in our fig. 33, we will take for the magnitude of L the expansion observed of the zone between 10° C and 17° C ($\Delta H_{17} - \Delta H_{10}$) and will divide it with the average of the maximum geographical gradients of these isothermal surfaces given by Seiwell. This gives:

$$\frac{74 \text{ m.} - 53 \text{ m.}}{\frac{1.33 \text{ m.} + 1.00 \text{ m.}}{2 \text{ km.}}} = 18 \text{ kilometers}$$

According to Seiwell (1937, p. 17), the normal geographical gradient is probably only one-half to one-third of the maximum gradient used in the above calculation. Making a maximum allowance, we will therefore multiply our result by about three, using 50 kilometers as our value of L. For the average thickness of the zone between 17° C and 10° C we will further use the mean depth of these isotherms recorded by Seiwell (*loc. cit.*, p. 13). The situation then appears to be as indicated in fig. 34.

Since we are not here concerned with the third dimension, we can deal with the problem in terms of integral velocity transport or area transport. What we have to account for is therefore the increase in area from $B_1\ B_2\ H_{17}\ H_{10}$ to $B_1\ B_2\ H'_{10}\ H'_{17}$ or:

$$\Delta H_{17} \times \frac{L}{2} - \Delta H_{10} \times \frac{L}{2} = \frac{(74 \text{ m.} - 53 \text{ m.}) \times 50 \text{ km.}}{2}$$

$$= 525{,}000 \text{ m}^2$$

This increase occurred over a vertical range between mean depths of the 17° C and 10° C isotherms of 388 meters, during 12½ hours or 45,000 seconds. The required increase in average lateral velocity per second at st. *2639* is therefore:

$$\frac{525{,}000 \text{ m}^2}{388 \text{ m} \times 45{,}000 \text{ sec.}} = 0.03 \text{ m. sec.}$$

or:

3 cm. pr. sec.

This average increase in lateral velocity is patently very reasonable whether one prefers to consider it reversible or not, but has absolutely no bearing upon the question of reversal or progression.

While Seiwell's data thus provide absolutely no reason for assuming vertical oscillations in preference to progressive horizontal displacements connected with the lateral translation required by Rossby's theory, Seiwell's findings of approximately six and twelve hour periods, however, tends to confirm the assumption of lunar periodicities in the pattern of movement regardless of their true character.

With regard to vertical displacements at greater depth, Seiwell quite properly remarks upon the fact that the decrease of the temperature gradients make the exact determinations of depth of isotherms very unreliable. It might be brought out, however, that when we consider the extreme range of recorded values, we include in our considerations also the extreme range of errors of observation, and are no longer operating even with probable errors only. Seiwell (*loc. cit.*, p. 6) allows an error of 0.01 to 0.02° C in the temperature observations, and if

the temperature gradients shown in his table (p. 28) are plotted on a large scale we see that an allowance of only 0.01° C extreme error for extreme observations will reduce the vertical range of the 3° C isotherm by more than 20 meters (10 + 10) from the range of 78 meters recorded by Seiwell (loc. cit., table 3, p. 13) and that of the 2.4° isotherm by 90 meters (40 + 50) from the recorded 185 meters. As above stated, this allowance is not optional but mandatory by

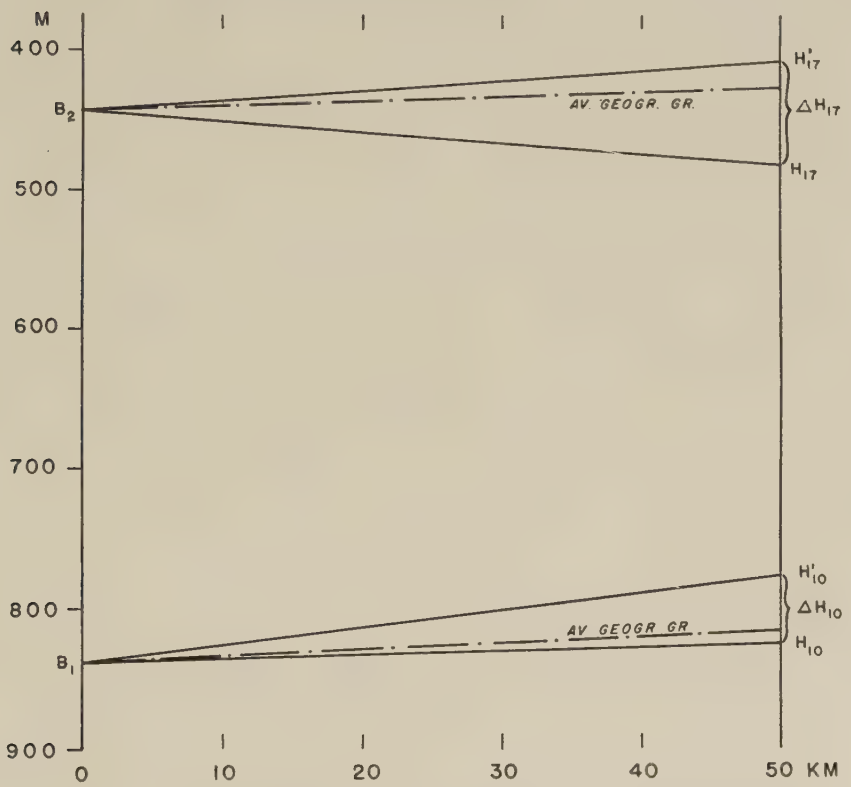


Figure 34. Analysis of possible volume changes indicated by Atlantis Station 2639.

comparison of extremes; and if we allow Seiwell's maximum extreme error of observation of 0.02° C, we see that the vertical diplacement of the 2.4° isotherm might disappear entirely. There is thus every reason to believe that vertical displacement decreases and disappears towards the depth and that a sufficiently deep boundary may be assumed to remain level for the purposes of such calculations of required volume transport and velocities as those carried out in the preceding.

TRANSVERSE MOVEMENTS AND DYNAMIC GRADIENT

If the preceding interpretation of the observations is approximately correct, it is easy to understand the discrepancy which develops between calculated and observed velocity distributions. When the transfer of the lighter water masses from right to left takes place, it obviously must cause a bulging of the normal dynamic surface gradient towards the left, and the relationship between the distorted transverse dynamic gradients thus developing and the longitudinal velocities of flow, which are not directly related to this distortion, can no longer

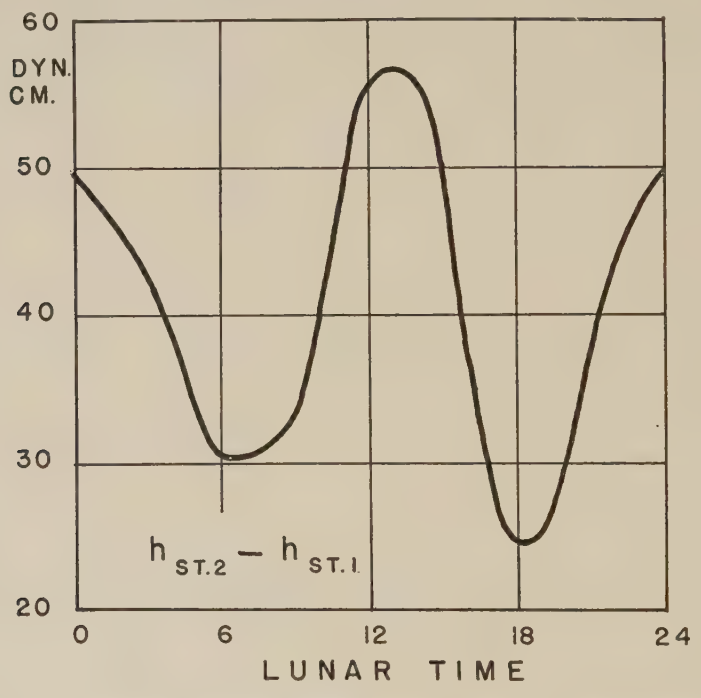


Figure 35. Variations in difference between stations 1 and 2 in dynamic height of free surface relative to 600 decibars.

be expressed in the simple terms of Bjerkness' velocity equation. The records of the anchor stations here reported upon thus provide an excellent example of a case in which the equation is only applicable to the calculation of the average velocity of the entire current, but not to the calculation of the velocity distribution, as already discussed on page 33 and 38.

It is of interest, however, to compare the variations in dynamic surface gradient between stations *1* and *2* as shown in fig. 35 with the time pattern of the extrusions. Immediately after the extrusion has become occluded (with

its posterior outer boundary more or less inverted against the outer boundary of the main current, fig. 32) the upper column at the second station contains only water of relatively low salinities and densities which must have entered

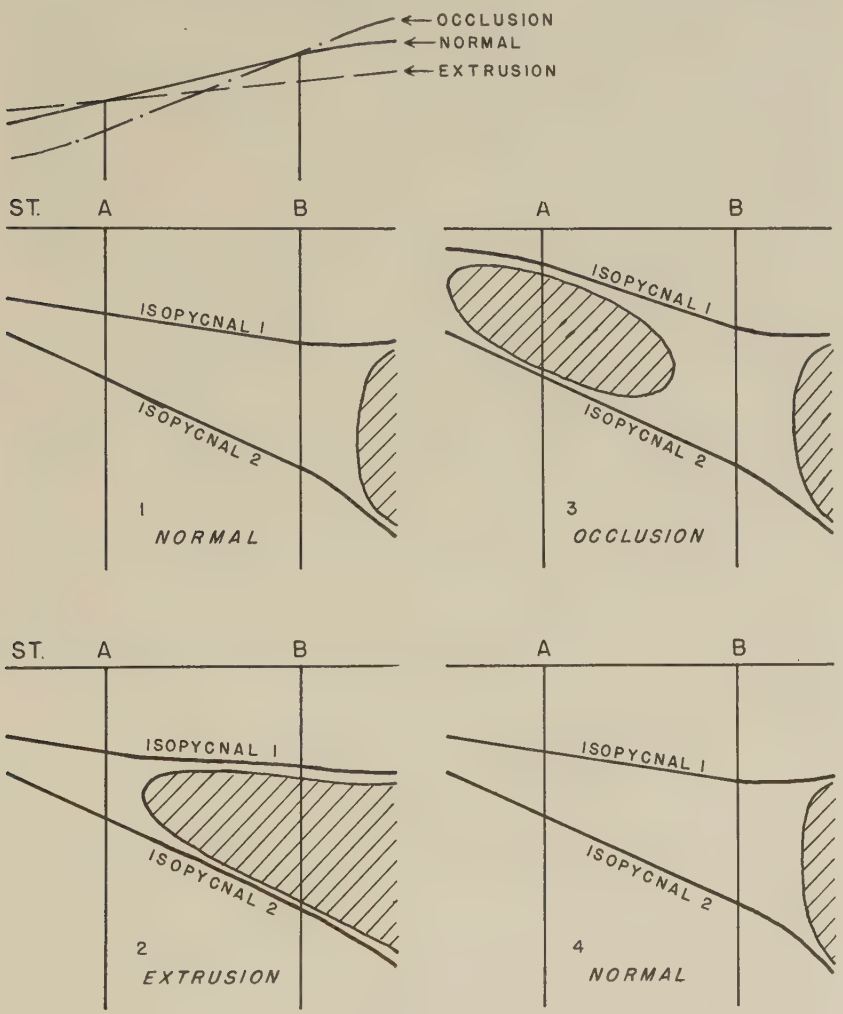


Figure 36. Effect of left lateral extrusion upon isopycnal and dynamic slopes. See text.

obliquely downwards from the left side of the current in the exchange caused by the extrusion. The calculated relative dynamic elevation of the surface at this boundary station of the main current therefore attains its maximum im-

mediately after the occlusion, and the average dynamic slope in the left marginal zone between station *1* and station *2* accordingly also attains its maximum at this time. These relationships are diagrammatically illustrated in figure 36; with variations in dynamic surface gradient between stations *A* and *B* shown at the top and with the complete cycle of corresponding transverse movements shown in four vertical profiles below. The movement occurs between isopycnals 1 and 2, sliding upwards over the lower isopycnal surface which is assumed to be unaffected. In the normal state the isopycnal surfaces slope downwards and the dynamic gradient of the free surface upwards from st. *A* to st. *B*. When the extrusion develops beyond st. *B*, it serves to raise the level of the upper isopycnal (1) and thereby also to lower the dynamic height of the free surface at this station. Since st. *A* is still beyond reach of the extrusion and therefore unaltered with regard to its characteristic, these changes at st. *B* must result in a reduction of slope both of the upper isopycnal and the free surface, and the average gradient energy between the two stations is at a minimum. When the occlusion occurs conditions at st. *B* revert to normal with regard to depth of isopycnals and height of free surface, but the arrival of the occluded body at st. *A* must simultaneously raise the level of the upper isopycnal and reduce the dynamic height of the free surface at this station, so that we now immediately after the occlusion must find the steepest transverse slopes both of upper isopycnals and free surface. In other words, the occlusion itself produces a maximum field of average gradient energy in the left marginal zone, which, if it has any direct relationship at all to actual velocities, however complex and inexpressible by the usual velocity equation, may immediately provide the conditions required to give impulse to the formation of a new extrusion, which reduces the marginal gradient again until it also itself becomes occluded. That is, the occlusion of an extrusion may directly provide the impulse for a new extrusion to develop.

SUMMARY AND CONCLUSIONS

Five 24 hour anchor stations were made in a series across the straits of Florida, each station being occupied for 24 hours with observations of temperatures and salinities at all depths every second hour; and surface velocities recorded by means of a taffrail log.

Temperature-Salinity correlation curves, and Salinity and Density Depth-Time profiles are given for all stations.

Lunar periodicities in water movements are strongly indicated in the hydrographic observations, particularly at the second station.

The methods of estimating volume transport are discussed; with emphasis upon the advantages of the direct estimates based only upon the two end stations of a profile.

It is pointed out that while Bjerkness' velocity equation may generally be

valid for the calculation of the average velocity over the entire width of the current, it may not be taken for granted that it will also be valid for the calculation of the transverse velocity distribution, since any lateral movements or transverse forces occurring under natural conditions will tend to distort the relationships between calculated dynamic gradient and actual velocities, without the same likelihood of affecting the average velocity over the entire width of the current. The observations at the anchor stations provide an excellent example both of the distortion of dynamic gradient relative to actual velocity distribution, and of the unaffected validity of the calculated average velocity in the presence of strong transverse movements.

Transverse profiles and horizontal time-space projections indicate the transverse movements to be in the nature of extrusions of lateral eddies to the left of the main flow as required by Rossby's wake stream theory of ocean currents.

It is suggested that the occurrence of these extrusions in point of time must be governed by the influence of tidal forces upon current velocities and that they therefore acquire at tidal periodicity, with the semi-diurnal period apparently predominant.

In conclusion, the author wants to state that while he fully recognizes the great amount of purely speculative deduction involved in the preceding interpretation of the recorded observations, he may also point to the fact that the observations in themselves are of such character that they require an exceptional amount of pure speculation to become comprehensible at all. While some doubt might attach to one or two individual observations, the general picture could only be changed by a complete rejection of 36 entire series of observations (see p. 39), and for such an extreme measure there are absolutely no reasonable grounds to be found in the records.

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SEASONAL STUDIES OF THE PHYTOPLANKTON OFF WOODS HOLE, MASSACHUSETTS [1]

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During the summer of 1935 certain investigations of the plankton in the waters near Woods Hole, Massachusetts, were undertaken by workers at the Oceanographic Institution. The zoöplankton studies have been described in the preceding paper by Clarke and Zinn (1937); the observations on phytoplankton form the subject of the present paper. At the outset five stations were established for regular observations, four in Vineyard Sound, and one in Buzzard's Bay. For the phytoplankton work water-bottle samples were taken at each station twice weekly, and at three depths, surface, mid-depth, and bottom. Along with these, determinations of the temperature, salinity, nitrate and phosphate content of the water were made.

During the first two months the water at all five stations was found to be so homogeneous in nature with regard to the phytoplankton, that it seemed unprofitable to continue observations at all stations. Therefore all subsequent collections were made at Station 3 alone, which is located at the Whistle Buoy near the western entrance to Vineyard Sound, Latitude 41° 17′ 35″, Longitude 71° 0′ 0″ (see Clarke and Zinn, 1937, for map). This station was chosen because conditions there, more nearly than at any of the others, simulate those of open waters, as will be seen later. From September, 1935, through the winter months samples were taken once a month; from April through July, fortnightly; during August, weekly. The final phytoplankton data were collected on August 20, 1936, giving a range of fourteen months for the entire survey. Samples were taken at the 2-meter, 15-meter, and 30-meter levels, the bottom being at 32 meters.

In this paper only such forms have been included as fall naturally within the plant classes, the chlorophyll-bearing or food-producing groups, which include the *Cyanophyceæ*, *Diatomaceæ*, *Dinoflagellatæ*, *Silicoflagellatæ*, *Coccolithineæ*, and certain of the pigmented flagellated groups. All of the true protozoan classes have been omitted.

In making the quantitative determinations of the phytoplankton

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for the majority of the samples Gran's centrifuging method was used, modified somewhat by having the organisms concentrated over a membrane filter, and then centrifuged. Since by this method others have found that there may be a 10 per cent loss of organisms, an original sample of 1,100 cc. was used instead of 1,000 cc. to allow for this error. For the winter and spring samples the precipitation method of Nielsen and von Brand (1934) was used chiefly because the amount of sample available was not sufficient to permit the use of the other method.

Most of the collections were made by Mr. Donald Zinn and the crew of the Oceanographic Institution boat *Asterias*. Chemical determinations were made by Dr. Homer P. Smith and Mr. Bostwick Ketchum. The writer is indebted to Dr. H. B. Bigelow and Dr. F. K. Sparrow, Jr., for certain guidance at the Woods Hole Oceanographic Institution, and to Dr. William R. Taylor and Professor H. H. Bartlett under whose direction the work was completed at the University of Michigan.

Hydrographic Observations

Certain physical features of the water, currents, tides, temperature, and salinity, play an undoubtedly important part in the distribution of plankton. The observations made on these factors during the present investigation have been presented by Dr. Clarke (Clarke, 1937; Clarke and Zinn, 1937). Although the control of phytoplankton species distribution, at least in part, must be attributed to the influence of temperature and salinity, no obvious correlations could be made between the variations in these factors and in the seasonal distribution of phytoplankton.

Nitrate determinations ranged from 4 milligrams of N. as NO_3 per cubic meter of sea water at 15 meters on October 1, to 62 milligrams at 2 meters on December 29 (see Figs. 1, 2, and 3). Through the summer months of the first year, the nitrate content of the upper strata of water was low, exhibiting slight fluctuations. Somewhat higher values were obtained in the lower strata. During the winter nitrates were gradually built up throughout the entire water mass to their highest concentration in early January. It is noteworthy that there is a decided lag in this accumulation of nitrates behind that of phosphates, a feature which is consistent with Cooper's theory (1933) based on observations in the English Channel, that the phosphates are returned directly to the water upon the decomposition of the plankton; whereas the nitrates are regenerated only after a series of intermediate steps. Terminating the winter accumulation, there was a sudden dropping off in the amount of nitrates in late January and early February, followed by a more gradual decrease throughout March and April. The summer was marked by small amounts of nitrates with

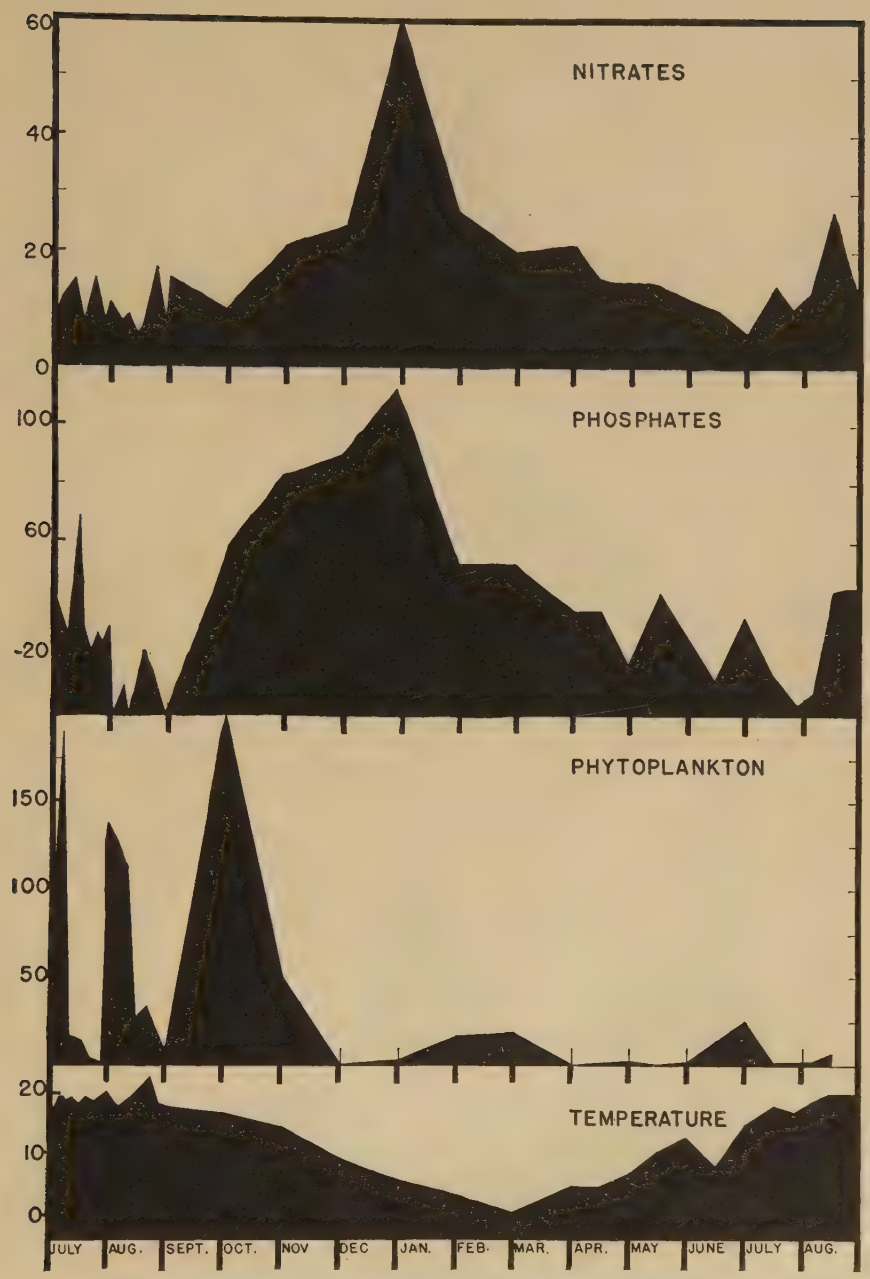

FIG. 1. Distribution of nitrates, expressed as milligrams of N as NO_3 per cubic meter of water; phosphates, as mg. of PO_4 per cubic meter; phytoplankton, in thousand cells per liter; and temperature, in degrees centigrade, at 2 meters depth, Station 3, from July, 1935, to Aug., 1936.

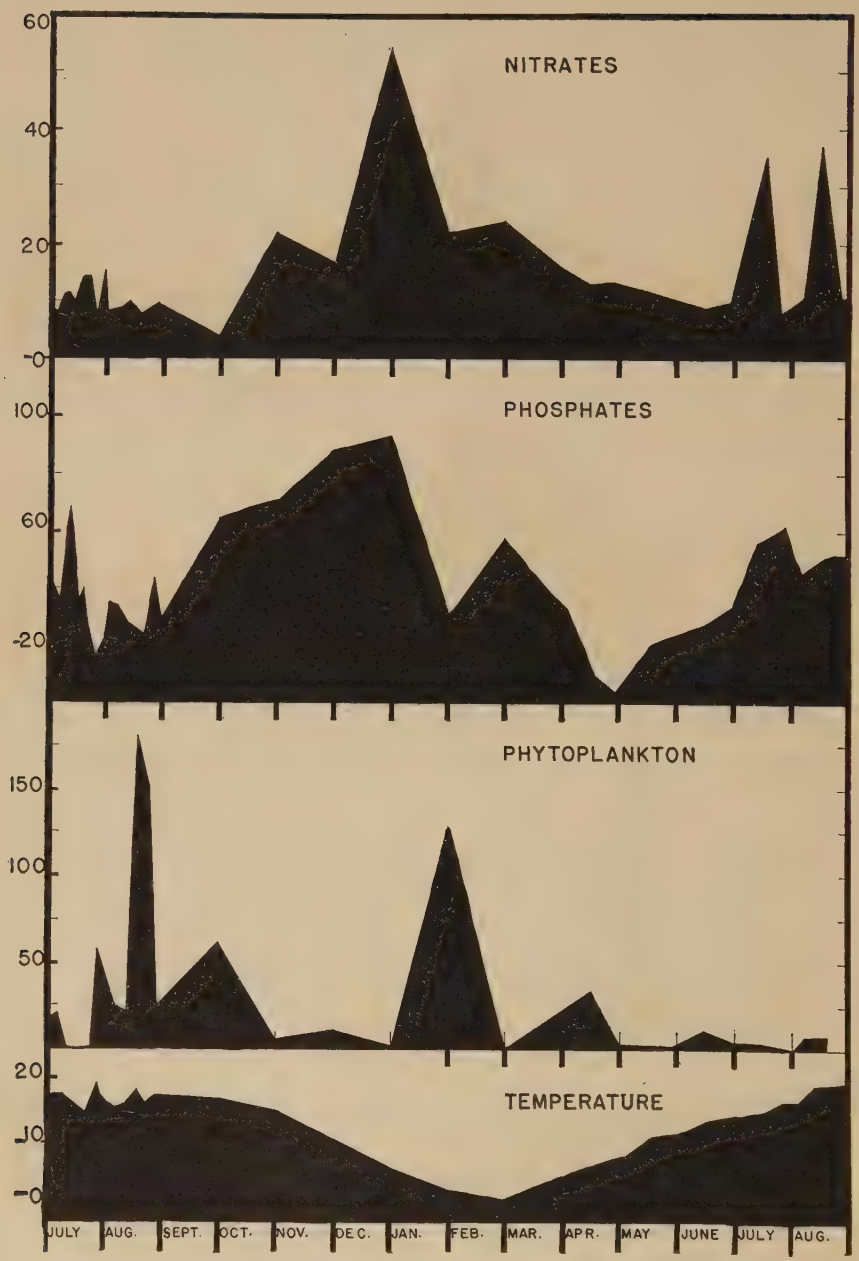

FIG. 2. Distribution of nitrates, expressed as milligrams of N as NO_3 per cubic meter of water; phosphates, as mg. of PO_4 per cubic meter; phytoplankton, in thousand cells per liter; and temperature, in degrees centigrade, at 15 meters, Station 3, from July, 1935, to Aug., 1936.

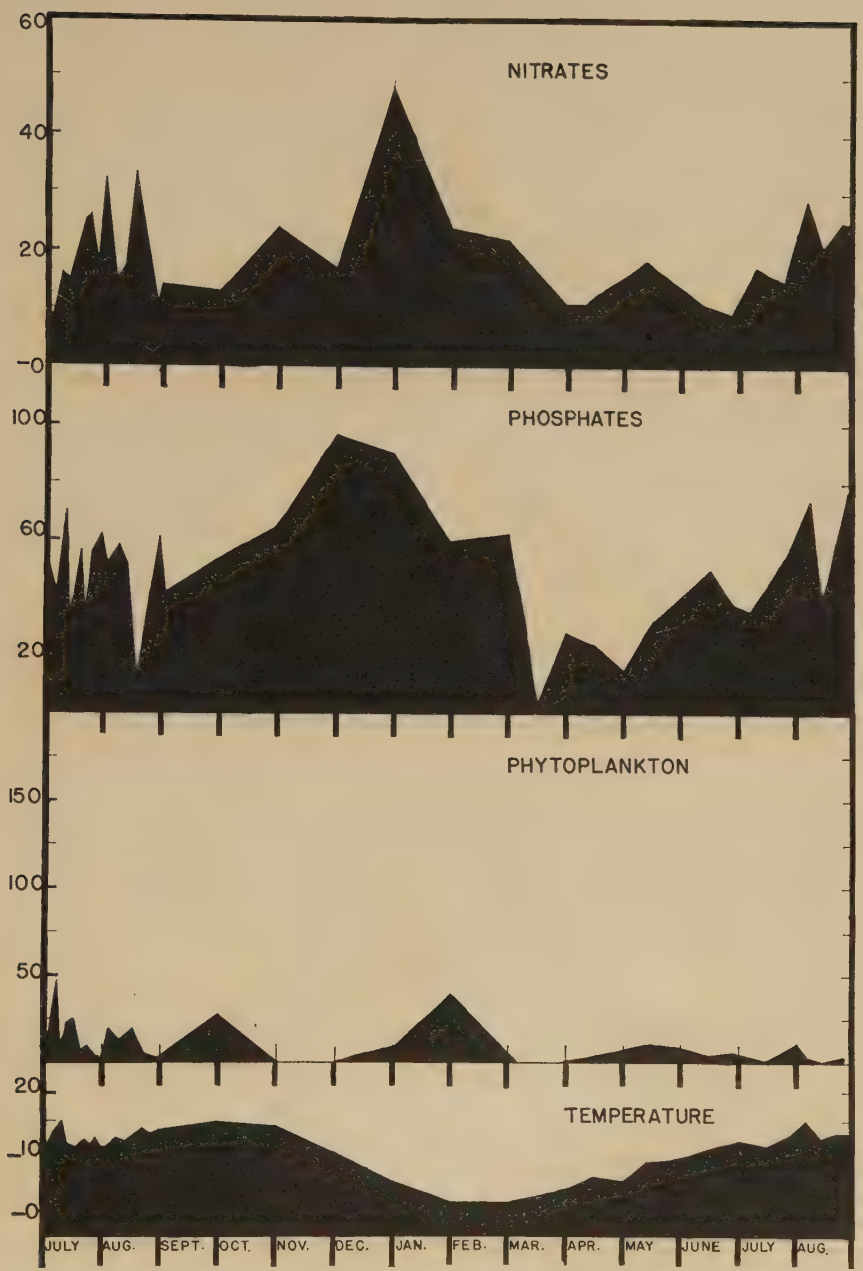

FIG. 3. Distribution of nitrates, expressed as milligrams of N as NO_3 per cubic meter of water; phosphates, as mg. of PO_4 per cubic meter; phytoplankton, in thousand cells per liter; and temperature, in degrees centigrade, at 30 meters, Station 3, from July, 1935, to Aug., 1936.

only slight fluctuations. In August there was an accumulation to form a second lesser peak, which again lagged behind the phosphates, and which was followed immediately by a decrease in concentration. Variations with depth were never extremely pronounced. However, there was usually some degree of stratification. From May through August, the nitrates tended to become concentrated at the bottom. By September they were more or less uniformly distributed, and remained so until December, when the surface waters became very rich in nitrates, the bottom waters much less so. This general relationship continued through April.

The phosphate distribution differed somewhat from that of nitrates. The total amounts found in the water were always much higher, though the total range was greater, from none in the surface waters through most of August and September, to 112 mg. PO_4 per cubic meter at the surface in December. The seasonal phosphate cycle was as follows: low through July and August of the first summer; increasing through September and October; reaching a maximum during the winter months of November, December and January; decreasing from the end of January through February and March, and dropping to the lowest point for the year in April, remaining low through May and June; in July and August gradually increasing, with another drop at the end of August. Stratification of phosphates was frequently much more pronounced than that of nitrates. From June through August the phosphates were found to be more concentrated at the bottom. In October the waters became more nearly uniform throughout, and remained so until spring, when the amounts at the surface increased over those at lower layers, this relationship remaining until June. The possible correlation of phytoplankton production with nitrates and phosphates will be discussed later.

Phytoplankton

(See Tables I and II)

The larger part of the phytoplankton in our collections was made up of diatoms, dinoflagellates, and flagellates. During certain seasons of the year members of the Silicoflagellatæ and Coccolithineæ became rather numerous, and stray members of the Cyanophyceæ appeared in the collections on occasion. More than 100 different species appeared during the year, divided among the several groups as follows:

Diatomaceæ	57
Dinoflagellatæ	31
Silicoflagellatæ	3
Coccolithineæ	2
Cyanophyceæ	2
Flagellatæ	?

TABLE I

Seasonal distribution of the more important phytoplankton species at 15 meters, Station 3, July, 1935, through August, 1936.

Species	Cells per Liter											
	July 5	July 15	July 25	Aug. 1	Aug. 12	Aug. 26	Sept. 3	Oct. 1	Nov. 2	Dec. 1	Dec. 29	Jan. 27
Diatomaceæ	....	....	....	....	....	....	....	....	....	....	....	....
Asterionella Bleakleyi	....	....	....	....	598	228	....	....	....	....	....	....
Chætoceros spp.	....	....	180	....	184	500	....	....	4,000	....	....	....
Ch. borealis	....	....	....	....	184	46	....	2,300	....	....	....	....
Ch. constrictus	....	....	1	....	138	1,496	....	500	....	....	....	....
Ch. decipiens	270	....	....	....	....	....	....	900	....	....	....	....
Ch. didymus	....	....	....	....	....	....	....	2,200	....	....	....	....
Corethron hystrix	....	....	....	138	36,708	2,048	....	....	....	....	....	....
Guinardia flaccida	....	....	....	322	1,196	....	....	100	600	200	....	....
Leptocylindrus danicus	....	....	....	....	4,874	....	....	2,300	....	700	....	....
L. minimus	....	....	....	....	42,964	....	....	300	....	....	....	....
Melosira sulcata	225	....	....	1,485	....	228	....	660	600	300	....	....
Nitzschia Closterium	90	....	46	....	3,108	228	....	....	....	....	....	....
N. seriata	135	....	....	....	14,306	368	....	17,600	3,600	5,800	....	....
Rhizosolenia alata	....	....	....	....	....	....	....	1,300	....	....	....	....
R. calcar-avis	....	....	....	138	....	....	....	....	100	....	....	....
R. fragillissima	....	....	....	....	....	....	....	800	....	100	....	....
R. hebatata semispina	270	....	46	....	....	....	....	300	200	....	....	330
Sceletonema costatum	....	....	....	506	46,782	1,035	....	30,000	....	....	....	....
Thalassionema nitzschioides	7,965	92	....	230	2,392	46	....	1,200	....	700	900	500
Thalassiosira Nordenskiöldii	225	....	....	1,196	276	405	....	800	....	300	300	3,800
Dinoflagellatæ	....	....	....	....	....	....	....	....	....	....	....	....
Gonyaulax tamarensis	90	....	....	....	322	....	1,300	....	....	....	....	....
Peridinium spp.	....	....	....	....	92	1,588	....	100	....	....	....	....
P. simplex	....	....	....	....	3,184	774	....	....	....	....	....	....
Prorocentrum minimum	6,480	92	598	3,780	2,832	2,502	....	....	....	....	....	....
P. Scutellum	....	....	....	368	966	319	....	....	....	....	....	....
Silicoflagellatæ	....	....	....	....	....	....	....	....	....	....	....	2,160
Distephanus speculum	1,755	....	....	184	....	....	....	100	....	....	....	....
Coccolithineæ	....	....	....	....	....	....	....	....	....	....	....	....
Syracosphæria	....	....	....	....	....	....	100	....	....	....	....	....
Flagellatæ	1,215	....	....	2,852	9,338	8,681	900	500	300	1,100	500	1,992
Total at 2 meters	189,000	16,000	35,000	136,000	30,000	19,400	9,300	214,000	53,000	1,000	4,900	16,000
Total at 15 meters	20,000	400	1,240	11,000	181,000	26,000	3,500	63,000	6,800	11,000	1,700	127,000
Total at 30 meters	45,000	19,000	9,800	2,900	21,000	2,070	....	28,000	500	200	7,300	39,000

TABLE I—*Continued*

Species	Cells per Liter											
	Feb. 23	Mar. 27	Apr. 13	Apr. 25	May 11	May 25	June 11	June 25	July 10	July 22	Aug. 6	Aug. 14
Diatomaceæ	....	....	....	....	....	....	....	....	....	....	....	....
Asterionella Bleakleyi	....	....	....	....	....	....	....	....	....	....	....	....
Chætoceros spp.	....	....	....	....	....	....	....	....	....	....	....	....
Ch. borealis	....	....	....	....	....	....	....	....	....	....	....	....
Ch. constrictus	....	....	....	....	....	....	....	....	....	....	....	....
Ch. decipiens	....	....	....	....	....	....	....	....	....	....	....	....
Ch. didymus	....	....	....	....	....	....	....	....	....	....	....	....
Corethron hystrix	....	....	....	....	....	....	....	....	....	....	....	500
Guinardia flaccida	....	....	18,500	....	....	....	....	....	....	300	300	1,200
Leptocylindrus danicus	....	....	....	....	....	....	....	....	....	....	....	....
L. minimus	....	....	....	....	....	....	....	....	....	....	....	....
Melosira sulcata	....	....	....	....	....	....	....	....	600	....	300	700
Nitzschia Closterium	....	....	....	....	....	....	....	....	....	....	....	....
N. seriata	....	....	....	....	....	....	....	....	....	....	....	....
Rhizosolenia alata	....	....	....	....	....	....	....	....	....	....	....	....
R. calcar-avis	....	....	....	....	....	....	....	....	....	....	700	700
R. fragillissima	....	....	....	....	....	....	....	....	....	....	....	....
R. hebatata semispina	200	....	....	....	....	....	....	....	....	....	....	....
Sceletonema costatum	....	....	....	....	....	....	....	....	....	....	....	....
Thalassionema nitzschioides	....	....	100	....	....	....	200	....	....	....	....	1,000
Thalassiosira Nordenskiöldii	....	....	....	....	....	....	....	300	500	....	....	500
Dinoflagellatæ	....	....	....	....	....	....	....	....	....	....	....	....
Gonyaulax tamarensis	....	....	....	....	....	....	....	....	....	....	....	....
Peridinium spp.	....	....	....	....	....	....	....	....	....	....	....	....
P. simplex	....	....	200	....	....	....	....	....	....	....	....	....
Prorocentrum minimum	....	....	....	....	....	....	....	200	200	....	800	100
P. Scutellum	....	....	....	....	....	....	....	....	100	....	200	200
Silicoflagellatæ	....	....	....	....	....	....	....	....	....	....	....	....
Distephanus speculum	....	....	....	....	....	....	....	....	....	....	....	....
Coccolithineæ	....	....	....	....	....	....	....	....	....	....	....	....
Syracosphæria	....	....	600	....	....	....	....	100	....	....	1,000	....
Flagellatæ	....	....	9,500	1,800	....	1,000	10,200	1,200	1,200	....	3,200	1,400
Total at 2 meters	19,000	500	2,300	2,800	200	2,500	15,600	26,000	2,500	2,600	2,800	7,150
Total at 15 meters	200	700	29,000	1,900	....	1,000	11,000	2,900	2,000	300	6,800	7,000
Total at 30 meters	....	....	....	5,700	11,000	9,200	3,300	5,900	1,300	12,000	300	800

Table II

Complete list of the species found at Station 3 during the survey of 1935–1936.

DIATOMACEÆ
Achnanthes tæniata
Asterionella Bleakleyi
japonica
Bacteriastrum hyalinum
Cerataulina Bergonii
Chætoceros spp.
affinis
borealis
borealis var. *concavicornis*
compressus
constrictus
curvisetus
debilis
decipiens
didymus
gracilis
laciniosus
teres
Cocconeis placentula
Corethron hystrix
Coscinodiscus centralis
excentricus
lineatus
Grammatophora marina
Guinardia flaccida
Hemiaulus Hauckii
Leptocylindrus danicus
minimus
Lichmophora abbreviata
Melosira moniliformis
sulcata
Navicula spp.
Nitzschia Closterium
longissima
seriata
Pleurosigma Normanii
Rhabdonema adriaticum
Rhizosolenia alata
calcar-avis
fragillisima
hebatata var. *semispina*
imbricata var. *Shrubsolei*
setigera
styliformis
Sceletonema costatum
Striatella unipunctata
Surirrella Gemma ?
Synedra Gallionii ?
Thalassionema nitzschioides
Thalassiosira decipiens
gravida
Nordenskiöldii
Thalassiothrix Frauenfeldii
longissima
DINOFLAGELLATÆ
Ceratium Fusus
lineatum
longipes
longipes var. *oceanicum*
macroceros
Tripos
Dinophysis acuminata
norvegica
Ovum
Exuviælla baltica
Glenodinium trochoideum
Gonyaulax tamarensis
Mesoporos asymmetricus [2]
Minusculus bipes
Noctiluca miliaris
Peridinium spp.
breve
Cerasus
conicoides
conicum
denticulatum
depressum
gracile
Granii
simplex
Phalocroma irregulare ?
Prorocentrum micans
minimum
Scutellum
SILICOFLAGELLATÆ
Dictyocha Fibula
Distephanus speculum
Ebria tripartita
COCCOLITHINEÆ
Rhabdosphæra tubulosa
Syracosphæra spp.
FLAGELLATÆ
CYANOPHYCEÆ
Glœocapsa
Oscillatoria

Both oceanic and neritic forms occurred with several important species belonging to either class. Neritic forms included both pelagic and bottom types; and occasional tychopelagic forms appeared.

The summer flora (see Table I) of 1935 was broadly typical of the area for that season. In July various species of *Chætoceros* were important. This is the normal summer flora for regions lying to the north of Woods Hole, and to be expected here. This genus was accompanied by *Corethron hystrix*, *Guinardia flaccida*, *Leptocylindrus danicus* and *Nitzschia seriata*, all temperate or boreal forms. In August these forms were replaced by species of *Rhizosolenia* (*R. calcar-avis*, *R. alata*, and *R. setigera*) and *Thalassionema nitzschioides*, a temperate flora. The summer maximum was reached during August, and consisted of *Rhizosolenia* and *Guinardia*. These are such large forms that the numbers recorded give a false impression of the actual state of the water. Plankton nets drawn through the waters during one of these maxima became clogged within a few minutes with *Rhizosolenia*. This summer maximum is very typical of the general area, and is similar to that found by Fish (1925). The entire flora

[2] Since the name *Porella* given by Schiller (1928) to a genus of the family Prorocentraceæ, Dinoflagellatæ, is identical with that of the well known liverwort genus *Porella* [Dill.] L., order Jungermanniales, and since this latter group antedates Schiller's genus by a great many years, it seems necessary to change the name of the dinoflagellate group. For this genus the name *Mesoporos* is offered her e in substitution for *Porella* Schiller. Since Schiller's generic name was not established by a Latin diagnosis, one is given here for the nomenclatorial validation of the genus, in accordance with the International Rules.

Mesoporos gen. nov.

Porella Schiller non *Porella* [Dill.] L.

Cellula ovalis plusminusve lateraliter applanata. Flagella per fenestram edentatam poriferem exserta. Hemitestae poro singulo mediano intus projecto praeditae, si lateraliter viso invaginationem conicam obtusam apice perforatam formanti. Chromatiphora dua vel tria flava vel brunneo-flava ad hemitestas applanata, absque pyrenoideis. Species 5, a cl. Jos. Schiller sub nomen Porellam descriptae, Arch. f. Protistenkunde 61: 54. 1928.

Mesoporos bisimpressus (Schiller) comb. nov.

Exuviælla bisimpressa Schiller, Arch. f. Protistenk. 38: 257. 1918. *Porella bisimpressa* ibid., **61**: 54. 1928.

Mesoporos asymmetricus (Schiller) comb. nov.

Porella perforata (Gran) Schiller, *Arch. f. Protistenk.*, **61**: 55. 1928. *Porella asymmetrica* Schiller, Dinoflagellata, Bd. 10, 3 Abt., S. 29, in Rabenhorst's Kryptogamen-flora. 1931.

Mesoporos globulus (Schiller) comb. nov.

Porella globula Schiller, *Arch. f. Protistenk.*, **61**: 56. 1928.

Mesoporos adriaticus (Schiller) comb. nov.

Porella adriatica Schiller, *Arch. f. Protistenk.*, **61**: 56. 1928.

Mesoporos perforatus (Gran) comb. nov.

Exuviælla perforata Gran, 1915, Bulk plankt. for 1912. Cons. Perm. int. p. l'explor. de la Mer, Copenhagen.

for this season was much more characteristic than that found in the following summer.

The winter flora, following the fall maximum, was extremely poor (see Table I). Collections made on October 1 showed a relatively large number of diatom species, occurring in considerable abundance. These collections were very similar to Fish's (1925) typical winter flora and indicate that the season of 1935 resembled those of 1922 and 1923 at that time. In October 1935 the species which Fish had found to be dominant were again dominant, namely, *Rhizosolenia alata*, *Sceletonema costatum*, and *Leptocylindrus danicus*. Certain of the forms which he mentions as occurring in abundance were found in our collections to be important here in October and at no other time throughout the winter (*Chætoceros decipiens* and *Rhizosolenia setigera*). This similarity is surprising in the face of the total lack of similarity throughout the rest of the winter.

For the rest of the winter months our collection showed that the plankton as a whole was extremely poor. The four important species, and at times nearly the only species found, were *Thalassionema nitzschioides*, *Rhizosolenia hebatata* var. *semispina*, *Thalassiosira Nordenskiöldii*, and *Nitzschia seriata*. All are boreal forms, the first two oceanic, and the last two neritic. Nearly all of the supplementary species were likewise boreal. Along with these forms there was a relatively high percentage of flagellated forms, a group which appeared throughout the year and which will be discussed later. These results are in the main very different from those of Fish (1925), who found a definite winter "maximum" consisting of a greater variety of abundant species than the summer.

It is extremely unfortunate that the great difficulty in making these collections necessitated the spacing of the trips rather far apart. During much of the year, because of the relative stability of the flora, this should have made little difference. Nevertheless it has resulted in our failing to observe any especial spring flowering of diatoms which may have occurred and which is so characteristic of the region north of Cape Cod. It is well known from the work of Bigelow, Gran and Braarud, and others that at some time during the early spring, and for a period of short duration, there is a flowering of diatoms dominated by *Thalassiosira Nordenskiöldii* in the Gulf of Maine, Bay of Fundy, and Massachusetts Bay, which results in phytoplankton numbers far in excess of those of any other season of the year. Fish seems not to have found a similar flowering, though he mentions *T. Nordenskiöldii* as occurring throughout January, February and March. However, the conditions with which he dealt at the Bureau of Fisheries' dock

were far different from those at our more off-shore station. He does, however, record the occurrence of a winter maximum beginning in November or December and lasting into March, for Vineyard Sound and Long Island Sound. Whether or not a flowering of either type occurred at our station during the spring of 1936 must remain problematic; certainly no such conditions appeared in our collections. It is entirely possible that in the interval between any two of our spring collections such a flowering could have burst forth and disappeared again without showing up at all in our collections. The weight of evidence which we have at hand seems to indicate that if such a flowering occurred during the spring of 1936, it could not have happened in all probability later than early February. Collections taken at the end of January show that the phytoplankton had increased decidedly over the winter months, yet was not abundant enough to be considered as a "flowering." Further, there was a decided increase in the number of cells of *T. Nordenskiöldii*. Other species which began to appear or to become prominent were *Rhizosolenia fragillissima*, *Nitzschia seriata*, *Thalassiosira decipiens*, *Thalassionema nitzschioides*, and certain of the peridinians, all boreal forms of the neritic or oceanic type.

By the end of January the nitrates and phosphates in the water had decreased markedly from their winter maximum concentration in December. Similar sudden depletions of these salts have been found by others in the English Channel, Loch Striven, and elsewhere (Harvey, 1928; Atkins, 1927; Marshall and Orr, 1929) to be coincident with the outburst of spring phytoplankton. It seems logical to infer that such an explanation may account for the sudden decrease in these salts at our station. The collections of late February and the following months show a marked falling off of the phytoplankton, and of the critical species, a condition which would normally follow the spring maximum. All of these arguments combine to indicate that any spring flowering of diatoms which may have occurred at our station must have done so between the end of December and the earlier part of February.

Following February the plankton became exceedingly scarce, and entered the summer period, which for 1936 was the poorest for the entire year. A few species of *Chætoceros*, which usually make up a large portion of the summer flora in this latitude, and which were prominent the year before, appeared early in the season but died out as the year progressed. The important species throughout the season was *Guinardia flaccida*, a temperate neritic form. The flagellates also became prominent for a time in June, and then decreased. Temperate

forms became more common; whereas boreal forms tended to die out. Certain of the smaller dinoflagellates appeared during the summer, though never in great numbers. The summer maximum, which is of very short duration, did not show up in our collections. However, we do have other information which gives the time and nature of this summer flowering. Collections made in another connection at the Oceanographic Institution showed that during a period of three or four days, from August 9 to August 11 or August 12 the waters in Vineyard Sound were teeming with a diatom flora which excluded nearly everything else, coloring the water a deep olive green. An examination showed this flowering to be made up almost entirely of the two large diatom species, *Rhizosolenia calcar-avis*, and *Guinardia flaccida*, both of which were prominent in the summer maximum of the year before. This growth appeared very suddenly and disappeared just as rapidly. As can be seen from our collections of August 6 and August 14, both species were present in the waters, but in very small amounts. Table I shows the general occurrence and abundance of the more important species found throughout the fourteen months at a depth of 15 meters.

Diatoms were obviously the most important element of the flora throughout the year. Dinoflagellates appeared throughout the year, more frequently in summer and fall, but their numbers were never sufficient to outweigh the diatoms. A group of forms which were exceedingly small, flagellated and pigmented, which therefore must be considered in a treatment of phytoplankton, kept appearing in all of our collections throughout the year, and in very large numbers. The formaldehyde used to preserve the collections apparently so distorted these forms that identification was impossible. There is no question that many widely separated organisms appeared in this class, which have been lumped together indiscriminately here under the term "Flagellatæ." At times certain of the forms were obviously swarm spores of certain of the diatoms and peridinians. It is quite possible that others may have been spores of other algal groups. Some were evidently independent flagellate forms. Much difficult work will be necessary before this general group can be clearly understood. No mention of such a prominent group as we have found seems to have gotten into the literature of this general region, probably because much of the previous work has been done with a no. 20 plankton net, which would allow these small types to slip through the meshes. Poor though our general grouping of the forms may be, it seems desirable to include them in this account because they doubtless play an important part in the general food cycle of the region.

In Table II is given a complete list of the phytoplankton found to occur at Station 3, during the survey.

Broadly speaking, then, our results correspond well with those of Fish, whose work is the only one of a similar nature conducted in a nearby region: Making allowances for the great differences between the two localities, and for the limits placed upon our collections, the seasonal cycle of the two surveys corresponds remarkably well. Comparison of the species given in Table II with those listed by Fish shows that a certain number of littoral or bottom forms appeared in his collections and not in ours. A number of these species appeared in our collections made during the first summer at the more littoral stations. Other features characteristic of more offshore waters are shown by our station. Along with stratification of the water column is seen a certain degree of stratification of phytoplankton. One of the outstanding characteristics of Fish's station is the homogeneity of the water from surface to bottom. The seasonal cycle at Station 3, if we consider that we have sufficient data from which to judge, more nearly resembles that of offshore waters, with its spring and fall maxima, and summer and winter lulls, than it does the neritic waters. Conditions here must be considered to be somewhat intermediate between the other two types.

For a long time oceanographers have held to the theory that phytoplankton production is tied up with and dependent upon the amounts of nitrates and phosphates found in the water in any given latitude. In a broad sense, although this does not seem to be the final factor which controls the cycle, there must be, certainly, some close correlation between the two. Some such broad relationship can be seen in the results of our survey. An examination of Figs. 1, 2, and 3 will show that the nitrates and phosphates were relatively plentiful during July and early August of 1935, and that they dropped suddenly during August. They gradually accumulated during the fall and rose to their highest point during the winter months. During January there was a sudden drop to a summer low which continued until July, when the salts began to accumulate again to a lower peak in August. Another decrease occurred here. Considering the curves for the plankton, it can be seen that there are certain points of correlation, assuming that the spring flowering occurred, as has been indicated earlier, before the beginning of February, and the summer one in the middle of August. When the phytoplankton was low, the salts began to accumulate. As the phytoplankton began to increase, the salts dropped off suddenly, implying that they were used up in the plant cells. The dying off of the phytoplankton was again followed by a

gradual accumulation of salts. These were no doubt supplied in part by the decomposition of dead organic matter, and in part by new water entering the Sound. There are minor differences between the curves throughout, but in the major phases this general relationship holds. Nitrates seem to be somewhat more critical for phytoplankton in these particular waters than phosphates. There was always more PO_4 in the water column than NO_3, probably always enough for some plant growth. It is with the curve for NO_3 that the phytoplankton shows the greatest correlation, and it may be that only when the PO_4 curve agrees with that of NO_3 in trend that it can be considered related to the plankton production. There is a much more pronounced relationship between the phytoplankton and the salts at 2 meters and 15 meters than at the bottom, the 15-meter level showing the clearest correlation. The general ratio of nitrates to phosphates which is shown by Redfield (1934) to exist in the open oceans, and which corresponds in general to the proportions in which these occur in plankton organisms, does not hold at our station. Our data reveal that throughout most of the year the phosphates exceeded the nitrates, a condition which is contrary to that normally found.

Quantitatively, a greater number of organisms were found near the surface than at the bottom. The greatest development of phytoplankton is usually found to be in the lower strata of water, but at our particular station the amounts of detritus found in the water at all levels was so noticeably greater than that found in more open waters, that it is quite possible that throughout much of the year light is not available at the lower levels for photosynthesis. It happened very frequently that the number of cells at the bottom greatly exceeded that at 15 meters. This is probably explainable by the fact that cells sink rapidly once they become inactive, hence the active cells are those at the surface; those at the bottom have become inactive or are dead. In general the important species found at all three depths at any one time were the same. No counts obtained during the entire survey were high, the highest number recorded being 214,000 cells per liter at the surface in October, a number which is normally much exceeded during the spring maximum at other localities. Doubtless the numbers during the spring flowerings which occur in this region would exceed 200,000 many times. The lowest number recorded was 200 cells per liter at 30 meters in December, and at 15 meters in February. Collections made in March for the entire water column were lower than at any other time of year.

This survey, incomplete though it is, and lacking two important phases of the phytoplankton cycle, adds definitely to our knowledge

of the waters near Woods Hole. It is the first study of the sort in this region of a station which is far enough from land to show some of the hydrographic features of the open sea. The quantitative work gives a reasonably accurate idea of the numbers of phytoplankton cells which occur in these waters at the different seasons; and the possible relationship between the plankton and the concentration of nitrates and phosphates is indicated.

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RELATION OF BACTERIA TO DIATOMS IN SEA WATER*

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The functions of the two major constituent groups of the phytoplankton, namely, the diatoms and the bacteria, are supplementary to one another in the cycle of life in the sea: the diatoms synthesize organic matter from the simple chemical substances produced in the decomposition or mineralization of organic matter in the sea by the bacteria. Although the general aspects of the activities of these two groups of organisms are fairly well known, their mutual interrelationships still remain to be determined. The following studies were carried out in an attempt to elucidate this important problem.

Methods

Four methods were used in these investigations: (1) Oxygen consumption in sea water enriched with diatom material; the oxygen being determined by a modification of the Winkler method. (2) Nitrogen transformation in the water, as a result of bacterial activities; the nitrogen being determined either directly as ammonia or indirectly, namely by an increase in oxygen consumption as a result of addition of glucose to the water; it had been previously found (Waksman & Carey, 1935) that the rate of glucose decomposition in sea water is controlled by the available nitrogen in the water. (3) Regeneration of the phosphorus, the latter being determined by the Atkins-Denigès method. (4) Increase in bacterial numbers, as measured by the plate method.

In most of the previous experiments on decomposition of organic matter in sea water (Waksman, Carey & Reuszer, 1933), excessive amounts of plankton material were added to the water. This resulted in appreciable changes in the aqueous medium, particularly the rapid consumption of the oxygen, whereby the system became changed from a purely aerobic to a distinctly anaerobic one. In the following experiments, mixed and pure plankton were added in concentrations not greatly in excess of those frequently found in natural sea water. Studies were also made of the transformation of marine plankton in the same vessel in which it had been synthesized.

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Decomposition of Dead Diatom Material by Bacteria

Two samples of diatom plankton consisting almost entirely of *Rhizosolenia* were collected in Vineyard Sound at Woods Hole. Analysed, on a dry basis, they gave 10·46 and 7·34 % carbon, and 1·52 and 1·05 % nitrogen, giving respective C : N ratios of 6·9 and 7·0; the phosphorus content of the mixed diatom material was 0·41 %, calculated as PO_4. These samples were mixed carefully and used in some of the following experiments.

Five and ten mg. portions of this plankton, in an air-dry state, were placed in standard glass-stoppered oxygen bottles of approximately 220 c.c. capacity. The bottles were filled either with fresh, filtered sea water or with the same sea water enriched with 10 mg. of glucose per litre. The bottles were then incubated in the dark under water at a temperature of 20–22° C. The process of decomposition was followed by removing some of the bottles at different time intervals and analysing them for their oxygen, phosphate and bacterial content.

The results reported in Table I are typical of those obtained in several other experiments. In the sea water alone, the familiar sequence of a rapid bacterial multiplication, which in this instance reached a peak within 2 days, followed by a sharp drop to a low and fairly constant level, occurred (Waksman & Carey, 1935; Waksman & Renn, 1936; Renn, 1937). Oxygen consumption was parallel with the increase in bacteria. Phosphate was also consumed during the logarithmic growth phase of bacterial multiplication; the lowest phosphate values coincided with the highest bacterial counts. However, as the bacterial cells began to die off and autolyse, phosphate was rapidly regenerated in the water. The increase of 20 mg. of PO_4 per $m.^3$ of sea water, at the end of 420 hr. of incubation, over the amount originally present, represents the phosphate liberated from the organic matter originally present in the sea water, either in true solution or suspension, and susceptible to bacterial attack.

In the water to which diatom material had been added, somewhat different results were obtained. Since the dead diatoms were an available food supply for the bacteria present in the water, a higher bacterial count was obtained than in the sea water alone. With 5 mg. of diatom material present, the maximum count of 1,440,000 bacteria per 1 c.c. was obtained in 36 hr. With 10 mg. of diatom material present, the maximum number of bacteria was 2,000,000 per 1 c.c. in 12 hr. This indicates that the dead diatom material was quickly attacked and decomposed by the bacteria. The phosphate content of the sea water increased continuously throughout the duration of the experiment. Although some phosphate was no doubt utilized by the bacteria in the synthesis of their cell substance, there was more phosphate liberated from the diatom material by the bacteria than they could themselves assimilate. There resulted, therefore, a gradual increase in the PO_4 content of the sea water. This inability of the bacteria to utilize all the phosphate that they had liber-

ated was due to an insufficient supply of available energy which limited bacterial multiplication, as will be shown later. At the end of 420 hr. the minimum increase in phosphate content of the sea water was 66 mg. per $m.^3$, due to the decomposition of 5 mg. of the diatom material per bottle and to autolysis of the subsequently synthesized bacterial substance. When 10 mg. of this material was used the phosphate increase was 111 mg. per $m.^3$ The amounts of phosphorus added in the diatom material were equivalent to 92·5 and 185 mg. PO_4 per $m.^3$ respectively. It can thus be seen that approximately two-thirds of the total PO_4 present in the diatom material was liberated into the sea water as a result of bacterial activities, within 420 hr. and usually within 132 hr.

It is interesting to compare these results with those obtained by Cooper (1935), who found soluble phosphate to be liberated rapidly in the decomposition of plankton material, but less rapidly with diatom material than with animal plankton.

When an additional energy supply was added to the sea water, in the form of glucose, a marked increase in oxygen consumption, phosphate utilization and bacterial multiplication took place in sea water with and without the addition of 5 mg. of diatom material. The phosphate content of the water in both cases dropped within 12 hr. to less than 30 mg. per $m.^3$, which is the lower limit of the analytical method. Regeneration of the phosphate did not occur until after 96 hr. of incubation when the bacterial numbers had been greatly reduced. That available nitrogen was liberated in the decomposition of the diatom material is best shown by the high bacterial count of 7,000,000 per 1 c.c. in the presence of glucose.

Since all or practically all of the PO_4 had been removed from the water in a very short time, in the presence of glucose, it was thought that it might be of interest to determine whether the lack of a sufficient supply of available PO_4 was a limiting factor in the decomposition of the diatom material by the bacteria. In the following experiment an excess of PO_4 was added to the sea water, and only 5 mg. portions of the diatom material were used. The results are reported in Table II. In the sea water alone and in the presence of diatom material, a consumption of 188 mg. PO_4 per $m.^3$ occurred within 60 hr. Within the same period of time, the sea water to which 10 mg. of glucose had been added showed a loss of 348 mg. of PO_4 per $m.^3$, whereas the sea water containing both diatom material and glucose showed a loss of 368 mg. PO_4 per $m.^3$ After 60 hr. a gradual regeneration of the phosphate took place. The greatly increased rate of oxygen absorption and phosphate utilization seems to indicate that the diatoms decomposed more rapidly in the presence of an excess of phosphate.

The results of these two typical experiments are thus sufficient to demonstrate clearly that dead diatoms can serve as a readily available food supply for bacteria, the diatoms being rapidly decomposed and the nitrogen and phosphorus rapidly liberated in available forms.

Table I. Decomposition of Dead Diatom Material in Sea Water by Bacteria

Incubation hours	Sea water alone: Oxygen consumed c.c./l.	Sea water alone: PO_4 γ/l.	Sea water alone: Bacteria in 1 c.c.	Diatom material 5 mg.: Oxygen consumed c.c./l.	Diatom material 5 mg.: PO_4 γ/l.	Diatom material 5 mg.: Bacteria in 1 c.c.	Diatom material 10 mg.: Oxygen consumed c.c./l.	Diatom material 10 mg.: PO_4 γ/l.	Diatom material 10 mg.: Bacteria in 1 c.c.	Glucose 10 mg.: Oxygen consumed c.c./l.	Glucose 10 mg.: PO_4 γ/l.	Glucose 10 mg.: Bacteria in 1 c.c.	Glucose 10 mg. + diatom material 5 mg.: Oxygen consumed c.c./l.	Glucose 10 mg. + diatom material 5 mg.: PO_4 γ/l.	Glucose 10 mg. + diatom material 5 mg.: Bacteria in 1 c.c.
0	0	126	10,400	0	126	10,400	0	126	10,400	0	126	10,400	0	126	10,400
12	0·04	131	690,000	0·50	135	1,410,000	0·78	147	2,000,000	0·62	< 30	470,000	1·02	< 30	2,200,000
24	0·15	128	770,000	0·67	143	900,000	1·35	149	1,290,000	2·66	< 30	2,180,000	3·40	< 30	7,600,000
36	0·19	98	850,000	0·90	149	1,440,000	1·41	—	1,310,000	3·69	< 30	2,170,000	4·32	< 30	5,200,000
48	0·33	—	—	1·02	—	—	1·72	—	—	3·98	—	—	4·66	—	—
60	0·38	135	600,000	1·05	148	1,150,000	1·96	173	750,000	4·20	< 30	730,000	4·97	< 30	1,860,000
96	0·50	—	—	1·59	171	61,000	2·56	192	142,000	5·69	64	35,000	5·74	82	260,000
132	0·78	144	6,100	1·92	209	—	2·66	244	109,000	5·80*	118	—	—	165	124,000
252	—	—	3,100	2·26	—	28,000	3·83	—	60,000	—	149	1,500	—	—	100,000
420	1·72	146	1,800	2·60	212	12,700	4·66	257	24,000	—	—	2,100	—	—	17,800

* Oxygen used up completely.

Table II. Influence of Available Phosphorus upon Decomposition of Dead Diatom Material

Incubation hours	Sea water alone: Oxygen consumed c.c./l.	Sea water alone: PO_4 γ/l.	Sea water alone: Bacteria in 1 c.c.	Diatom material 5 mg.: Oxygen consumed c.c./l.	Diatom material 5 mg.: PO_4 γ/l.	Diatom material 5 mg.: Bacteria in 1 c.c.	Glucose 10 mg.: Oxygen consumed c.c./l.	Glucose 10 mg.: PO_4 γ/l.	Glucose 10 mg.: Bacteria in 1 c.c.	Glucose 10 mg. + diatom material 5 mg.: Oxygen consumed c.c./l.	Glucose 10 mg. + diatom material 5 mg.: PO_4 γ/l.	Glucose 10 mg. + diatom material 5 mg.: Bacteria in 1 c.c.
0	0	1,404	550	0	1,404	550	0	1,404	550	0	1,404	550
16	0·37	1,388	42,000	0·53	1,384	730,000	0·37	1,400	86,000	0·70	1,400	620,000
24	0·65	—	77,000	1·02	—	550,000	1·16	1,328	590,000	2·30	1,304	5,300,000
36	0·82	1,392	110,000	1·28	1,340	1,460,000	3·04	1,248	1,110,000	3·73	1,192	5,700,000
48	0·93	—	199,000	1·56	1,224	690,000	3·78	1,180	1,710,000	4·47	—	5,800,000
60	1·02	1,216	147,000	1·74	1,216	630,000	4·24	1,056	1,690,000	5·15	1,036	6,000,000
108	1·38	1,316	41,000	2·33	1,376	—	5·38*	1,128	640,000	—	1,288	1,000,000
264	2·02	1,448	9,800	3·33	1,392	42,000	—	1,336	174,000	—	1,448	188,000

* Oxygen used up completely

Relationship of Bacteria to Living Diatoms

In these investigations diatom cultures containing bacteria, bacteria-free diatom cultures and freshly collected mixed diatom plankton were used.

A culture of *Nitzschia closterium* originally obtained from Dr E. J. Allen, of the Plymouth Laboratory, was grown on the standard nutrient Miquel-Allen medium, in 500 c.c. Erlenmeyer flasks, for a period of 20–30 days. The contents of several flasks were combined, centrifuged and washed with fresh sea water, again centrifuged and the residue suspended in sea water. Varying amounts of the diatom suspension were added to 220 c.c. oxygen bottles containing fresh sea water. The bottles were incubated in the dark, at room temperature under water, and analysed at various intervals. The bacterial content of 1 c.c. of the concentrated *Nitzschia* material was 4,800,000 and the diatom content 18,400,000; the fresh sea water contained 12,000 bacteria in 1 c.c. The results presented in Table III show that the *Nitzschia* cells added to fresh sea water underwent a certain amount of oxidation; this was accom-

Table III. Relation of Bacteria to Enriched Culture of *Nitzschia closterium* added to Sea Water

Nitzschia culture added per litre* c.c.	Oxygen consumed c.c. per litre				Bacteria in 1 c.c.			Phosphate γ per litre	
	1 day	3 days	6 days	8 days	1 day	3 days	8 days	6 days	8 days
0	0·48	0·69	0·90	—	850,000	750,000	30,000	70	—
2·3	0·66	2·19	2·79	3·39	690,000	575,000	46,000	110	210
4·5	0·81	2·52	5·16	5·22†	800,000	2,750,000	76,000	420	380
9·0	1·05	2·34	5·22†	5·22†	650,000	405,000	825,000	300	680

* The dry matter content in the *Nitzschia* suspension was calculated from the total nitrogen (0·14 mg. per 1 c.c.) to be equivalent to 1 mg. organic carbon in 1 c.c.

† Oxygen used up completely.

panied by the liberation of phosphate, but not by an appreciable increase in bacterial numbers. The increased consumption of the oxygen may have been due partly to the respiration of the diatoms and partly to bacterial decomposition. Maximum bacterial multiplication and phosphate liberation were obtained after 8 days, with the highest concentration of the *Nitzschia* cells. At this stage, practically all the phosphate present in the *Nitzschia* material had been regenerated, as is easily calculated from the N/PO_4 ratio of 7/3; this ratio was found for the mixed diatom plankton. Dr H. W. Harvey‡ has suggested that it is quite possible for some of the phosphate to be introduced as precipitated ferric phosphate with the *Nitzschia* culture, which would account in part for the high phosphate recovery.

This experiment was repeated, using younger (12-day-old) cultures of the diatom material and concentrating it by centrifuging, to give a preparation

‡ Personal communication.

which contained 9,200,000 *Nitzschia* and 3,100,000 bacteria per 1 c.c. The results of this experiment (Table IV) confirmed the previous observation that, in the presence of a living culture of *Nitzschia*, the bacterial activities were very limited. No nitrogen was liberated, as shown by the fact that the addition of glucose to the cultures brought about no increase in oxygen consumption: with 2·3 c.c. *Nitzschia* suspension added per litre of water, the increase in oxygen consumption was, without glucose, 0·87 c.c. and with glucose 0·72 c.c.; with 4·5 c.c. of the diatom culture, the corresponding increases were 2·10 and 1·29 c.c. respectively. The addition of nitrate to the water did not stimulate to any great extent the destruction of the diatoms.

In order to eliminate the interfering factor which might have resulted from the introduction into the fresh sea water of large numbers of bacteria, and also for the purpose of determining the consumption of oxygen as a result of diatom respiration, bacteria-free cultures of the diatom were used.

TABLE IV. INFLUENCE OF NITROGEN AND GLUCOSE ON THE OXIDATION OF *NITZSCHIA CLOSTERIUM*

Nitzschia culture added per litre c.c.	Nitrate nitrogen added per litre mg.	Glucose added per litre mg.	Oxygen consumed c.c. per litre			Nitrate N mg. per litre		Bacteria in 1 c.c.
			2 days	6 days	10 days	2 days	6 days	6 days
0	0	0	0·39	0·63	0·78	0·01	0·01	12,000
2·3	0	0	0·63	1·20	1·65	0·01	0·01	18,000
4·5	0	0	0·81	1·56	2·88	0·01	0·01	19,000
9·0	0	0	1·05	3·45	5·16*	0·01	Trace	450,000
0	0·07	0	0·45	0·69	0·69	0·10	0·10	—
4·5	0·07	0	0·93	2·01	2·85	0·01	Trace	—
9·0	0·07	0	1·47	3·81	4·62	0·01	Trace	—
0	0	5	0·63	1·62	2·52	—	—	55,000
2·3	0	5	0·69	2·16	3·24	—	—	70,000
4·5	0	5	0·63	2·34	3·81	—	—	330,000

* Oxygen used up completely.

A culture of *Nitzschia closterium* was obtained from Dr C. B. van Niel. It was grown for 13 days in Miquel solution, centrifuged and washed with fresh sterile sea water under sterile conditions and resuspended in sterile sea water. There were 8,500,000 diatom cells in 1 c.c. of suspension. One-half and 2 c.c. portions of this suspension were placed in oxygen bottles and filled with paper filtered sea water, previously kept overnight in the laboratory. In order to determine the oxygen consumption due to the respiration of the diatoms, controls containing the same amounts of diatom suspension were placed in sterile oxygen bottles, and filled with sea water which had been previously sterilized by heating at 15 lb. pressure for 20 min. The oxygen content of the sterile sea water was less than that of the fresh sea water due to the difficulty encountered in resaturating the water with oxygen after sterilization. All the bottles were placed in the dark under water and analyses made at different intervals. The results given in Table V show that during the first 88 hr. of

incubation the excess oxygen consumption in the sea water containing 2 c.c. diatom suspension over the oxygen consumption in the sea water alone can be accounted for by the respiration of the diatoms, since the sea water plus 2 c.c. diatom suspension consumed 1·81 c.c. oxygen per litre and the sea water alone 1·53 c.c. per litre, while the consumption of oxygen in the sterilized sea water plus 2 c.c. diatom suspension was 0·35 c.c. per litre. By adding the latter two figures, a consumption of 1·88 c.c. oxygen per litre is obtained; this is very close to the 1·81 c.c. oxygen consumed in the fresh sea water to which the diatom suspension had been added.

A microscopic examination of the centrifuged sediment at this point revealed that the diatoms were in all cases in good physical condition (chromatophores intact). It may therefore be concluded that living diatoms are not attacked by the bacteria. However, the bacterial counts showed that a greater

Table V. Relationship between Pure Cultures of Living Diatoms and Bacteria

	Fresh sea water		Fresh sea water +0·5 c.c. diatom culture		Fresh sea water +2 c.c. diatom culture		Sterile sea water + 0·5 c.c. diatom culture	Sterile sea water + 2 c.c. diatom culture
Incubation hours	Oxygen consumed c.c./l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	Oxygen consumed c.c./l.
0	0	400	0	400	0	400	0	0
20	0·34	1,000	0·40	185,000	0·74	10,000	0·06	—
42	0·80	39,000	0·80	133,000	1·03	312,000	0·14	0·34
88	1·53	—	1·55	—	1·81	—	0·17	0·35
136	1·84	74,000	2·18	81,000	2·74	98,000	0·23*	0·46*
184	2·10	77,000	2·42	158,000	2·96	107,000	0·46*	0·55*
256	—	—	—	—	—	—	1·03*	1·03*
20 days	2·33	900	2·99	3,700	3·69	9,200	—	—

* Water became contaminated with bacteria.

development of bacteria took place in the presence of the diatoms than in their absence. This confirms the previous observations of Gran (1933) that there is a certain parallelism between the development of diatoms and bacteria in sea water.

After 136 hr. incubation, an examination of the centrifuged sediment showed that the diatoms in the unsterilized sea water were badly disintegrated. The chromatophores were completely gone in many cases, and the cells were difficult to see because of changes in refractive index due to death. A number of Protozoa were found to be present in the water. The bacterial numbers showed a decreasing population, with the exception of the untreated sea water in which the peak had not yet been reached. Unfortunately, at this point, the sterile sea water to which the diatom culture had been added became contaminated with bacteria.

A comparative study was now made of the relationship of bacteria to living

and dead diatoms added to fresh sea water. Two series of oxygen bottles, one with and one without 5 mg. glucose per litre, received sea water enriched with PO_4 (100 mg. per m.^{3}). Each series was divided into three sets: (1) sea water alone; (2) 2 c.c. of a concentrated suspension of living *Nitzschia* (16,000,000 diatoms per 1 c.c. of suspension); (3) the same amount of diatom material, heated at 60–62° C. for 45 min. in order to kill the diatoms.

The results presented in Table VI show that the living diatoms and not the bacteria were the agents responsible for the rapid phosphate consumption. This is definitely demonstrated by the fact that the control sea water having, after 1 day, a higher bacterial count than the sea water with the 2 c.c. of living diatoms, showed a PO_4 consumption of only 28 mg. per m.^{3}, as compared with the complete or almost complete consumption of the 298 mg. of PO_4 in the sea water with the living diatoms. This fact is even more sharply brought out in the water containing glucose. In spite of the presence of glucose, which so readily stimulates bacterial multiplication, the bacterial count in the sea water plus living diatoms remained relatively low, while the phosphate and oxygen were rapidly consumed. Living diatoms can therefore be considered as successful competitors of bacteria for the available nutrients, and may represent one of the factors which tend to limit bacterial multiplication in the sea. The process of initial phosphate utilization and subsequent regeneration is again clearly indicated. On the 5th day, a sharp increase was found in the number of bacteria in the water receiving living diatoms. A microscopic examination of the centrifuged material showed that the diatoms had disintegrated in large measure. The bacterial increase was therefore due to the decomposition of the dead diatoms.

Relationship of Bacteria to Fresh Marine Plankton

Five samples of plankton were obtained by means of a No. 20 silk net on August 3–4 1936, one at a station in Nantucket Sound (No. 1) and four at stations on George's Bank (Nos. 2–5). The plankton was washed free from sedimentary material, using fresh sea water. It was then allowed to settle and concentrated plankton thus obtained. Different amounts of the freshly collected samples of plankton were added to a series of oxygen bottles containing fresh sea water obtained from the same stations. The bottles were incubated in the dark, and analysed for oxygen, bacterial numbers and phosphate. Sample No. 1 contained 10,536 diatoms per 1 c.c., mostly *Chaetoceras*, *Skeletonema* and *Rhizosolenia*; sample No. 2, 3,159 diatoms, mostly *Rhizosolenia*; No. 3, 19,025, No. 4, 24,450, and No. 5, 16,925, mostly *Rhizosolenia* and *Nitzschia*. The plankton of the last three stations consisted almost entirely of diatoms. The carbon content of the plankton was calculated from the nitrogen content using the ratio of C : N = 7 : 1. The results presented in Table VII show that considerable oxygen consumption took place in all cases; the phosphate was liberated in a soluble form. These processes were not

Table VI. Relationship between Bacteria, and Living and Dead Diatoms in Sea Water

100 γ PO_4 added per litre

Incubation days	Sea water alone: Oxygen consumed c.c./l.	Sea water alone: PO_4 γ/l.	Sea water alone: Bacteria in 1 c.c.	Living diatoms*: Oxygen consumed c.c./l.	Living diatoms*: PO_4 γ/l.	Living diatoms*: Bacteria in 1 c.c.	Dead diatoms*: Oxygen consumed c.c./l.	Dead diatoms*: PO_4 γ/l.	Dead diatoms*: Bacteria in 1 c.c.
0	0	298	400	0	298	400	0	298	400
1	0·14	270	184,000	0·40	< 30	117,000	0·94	270	430,000
3	0·57	282	5,000	0·97	< 30	190,000	1·20	280	20,000
5	0·62	298	20,000	1·42	185	70,000	1·93	314	18,000
7	0·80	301	5,700	1·77	319	26,000	2·11	338	11,700

5 mg. glucose and 100 γ PO_4 per litre

Incubation days	Sea water alone: Oxygen consumed c.c./l.	Sea water alone: PO_4 γ/l.	Sea water alone: Bacteria in 1 c.c.	Living diatoms*: Oxygen consumed c.c./l.	Living diatoms*: PO_4 γ/l.	Living diatoms*: Bacteria in 1 c.c.	Dead diatoms*: Oxygen consumed c.c./l.	Dead diatoms*: PO_4 γ/l.	Dead diatoms*: Bacteria in 1 c.c.
0	0	298	400	0	298	400	0	298	400
1	1·71	< 30	2,080,000	0·77	< 30	52,000	1·99	< 30	710,000
3	2·63	170	8,000	2·05	< 30	35,000	3·76	167	90,000
5	3·36	203	5,000	3·26	< 30	141,000	4·39	258	51,000
7	3·53	237	11,000	3·93	94	158,000	4·79	256	8,500

* 2 c.c. of concentrated diatom culture, containing 16,000,000 *Nitzschia* cells in 1 c.c.

always accompanied by corresponding increases in bacterial numbers, especially in the diatom-rich plankton. With the exception of Station 3, there was a certain parallelism between the concentration of the plankton in the samples and the rate of oxygen consumption. The plankton of Station 1 and to some extent of Station 2 was rich in copepods, which may account for the greater abundance of bacteria in the water receiving these two samples of plankton. The most significant result of this experiment is the lack of correlation between oxygen consumption in the water receiving diatoms and bacterial multiplication.

TABLE VII. RELATION OF BACTERIA TO FRESHLY COLLECTED MIXED DIATOM PLANKTON

Station no.	Plankton added per litre c.c.*	Oxygen consumed c.c. per litre			Bacteria in 1 c.c.				Phosphate γ per litre
		1 day†	3 days	7 days	Start	1 day	3 days	7 days	7 days
1	0	0·78	—	—	20,100	1,160,000	—	28,000	30
1	4·5	0·88	1·41	1·77	32,200	2,170,000	49,000	21,000	40
1	9·0	1·14	1·53	1·89	—	2,250,000	72,000	25,500	40
1	22·5	1·18	1·77	1·98	—	2,450,000	81,000	22,000	120
2	0	0·51	—	0·83	5,800	279,000	—	46,500	40
2	4·5	0·48	0·99	1·25	7,200	307,000	75,000	72,000	60
2	9·0	0·62	1·35	1·79	—	740,000	131,000	52,500	50
2	22·5	1·29	2·97	3·77	—	2,030,000	270,000	39,000	150
3	0	0·42	—	0·99	4,200	1,050,000	—	62,000	50
3	4·5	0·61	1·03	1·65	24,000	915,000	240,000	57,500	80
3	9·0	0·65	1·71	1·74	—	990,000	375,000	59,500	90
4	0	0·39	—	0·90	12,400	940,000	—	38,500	70
4	4·5	0·75	1·38	1·98	9,500	—	355,000	65,000	80
4	9·0	0·91	2·14	3·15	—	980,000	245,000	—	—
5	0	0·31	—	0·84	2,700	550,000	—	109,000	30
5	4·5	0·54	1·71	2·88	6,600	790,000	330,000	56,000	100
5	9·0	0·57	2·75	5·01	—	1,720,000	365,000	51,000	120

* The carbon content of 1 c.c. of the five samples of plankton were as follows: No. 1, 0·05 mg.; No. 2, 0·06 mg.; No. 3, 0·37 mg.; No. 4, 0·22 mg.; No. 5, 0·23 mg.
† 42 hr. for Station 1.

RELATION OF BACTERIA TO FRESHLY SYNTHESIZED DIATOM MATERIAL

It has been shown previously (Waksman & Renn, 1936) that the processes resulting from diatom oxidation in sea water could be better elucidated, if growth of the diatoms was first permitted to take place in closed containers, and photosynthesis then stopped by placing the containers in the dark. Conditions are thus obtained which approach more nearly those found in nature. In order to increase the amount of synthesized diatom material above that normally present in sea water, an enriched medium was employed. This consisted of fresh sea water, to which 5 mg. KNO_3, 2 mg. K_2HPO_4 and 2 mg. $FeCl_3$ had been added per litre. The enriched water was distributed in glass-stoppered oxygen bottles, and these incubated at room temperature, under water and in the light, in glass aquaria. After different periods, a few of

the bottles were removed. Some were analysed at once and some were transferred to a water bath kept dark at room temperature, and allowed to remain under water for 5–12 days. In those bottles, where extensive photosynthesis took place, the water became supersaturated with oxygen, some of which being liberated in a gaseous form, was lost, thus modifying the results of some of the oxygen determinations.

Gradual consumption of the oxygen took place in those bottles which were incubated in the dark (Table VIII). In the light, oxygen was rapidly liberated, due to the photosynthetic activity of the diatom population in the enriched sea water; after 7 days, the nitrate disappeared completely; the phosphate was present in excess of the requirements of the diatoms; the oxygen increased by 4·62 c.c. per litre of water. When the bottles were now placed in the dark,

Table VIII. Synthesis and Oxidation of Diatom Material in Enriched Sea Water*

Incubation of bottles, days		On basis of 1 litre of water			
		Oxygen above (+) or less (−) than the control	Phosphate		
Light	Dark	c.c.	Left γ/l.	Regenerated as a result of incubation in the dark γ/l.	Bacteria in 1 c.c.
7	—	+4·62	420	—	145,000
7	2	+3·54	500	80	72,000
7	11	+1·98	460	40	6,000
13	—	+9·39	260	—	103,000
13	5	+8·37	310	50	120,000
13	12	+5·74	330	70	35,000
—	7	−0·30	890	—	30,000
—	13	−0·42	760	—	72,000

* The nitrate nitrogen added and found in control water was 0·76 mg. per litre; it completely disappeared in the bottles incubated for 7 days in the light.

there was a reduction of 1·08 c.c. in the oxygen content per litre in 2 days, and of 2·64 c.c. in 11 days. When photosynthesis was allowed to proceed for 13 days, the oxygen content of the water increased by 9·39 c.c. per litre; incubation in darkness following this period resulted in a decrease of 1·02 c.c. in oxygen concentration in 5 days, and of 3·65 c.c. oxygen in 12 days. The consumption of phosphate in the light was 470 (890–420) γ per litre in 7 days, and 500 (760–260) γ in 13 days. When oxidation of the diatoms began, the phosphorus was regenerated as phosphate, but only very slowly. The gradual disappearance of the phosphate in the water kept in the dark was due either to its partial consumption or to its precipitation as insoluble phosphate, as a result of addition of iron, as ferric chloride.

Considerable variation was found among the individual bottles in the previous experiments. This may account for some of the discrepancies obtained in certain determinations. In order to check this, the results of another

experiment are reported here. In this, all the determinations were made at least in duplicate and sometimes in triplicate; the analyses were also carried out at more frequent intervals (Table IX). Only one concentration of nitrate was used, namely 5 mg. KNO_3 per litre. The maximum amount of photosynthesis, as measured by the oxygen liberated, was attained in 7 days; nitrate assimilation continued even after the maximum was attained. At that time, oxidation of the synthesized material seemed to coincide with assimilation. When photosynthesis was stopped, by incubating the bottles in the dark, rapid oxidation of the diatoms took place, especially at the 5–7 day periods when the diatom population in the water was carrying out its most active

TABLE IX. RELATION OF BACTERIA TO OXIDATION OF DIATOM PLANKTON

Incubation of bottles, days		Oxygen content per litre	Nitrate N per litre	Phosphate γ per litre		Bacteria
Light	Dark	c.c.	mg.	Left	Regenerated	in 1 c.c.
0	0	5·38	0·84	850	—	12,000
3	0	7·65	0·41	700	—	182,000
3	5	7·07	—	750	50	31,000
5	0	15·18	0·11	490	—	—
5	5	9·51	0·13	670	180	—
7	0	17·47	0·16	470	—	132,000
7	5	12·27	—	610	140	15,000
10	0	17·42	0·03	340	—	126,000
10	5	12·62	—	—	—	28,000
12	0	17·66	—	340	—	42,000
12	5	13·06	—	—	—	75,000

photosynthesis. The ratio between nitrogen and phosphate assimilation, for the first three days of photosynthesis, was $\frac{0·43}{0·15}$ or 2·9 : 1, and for the 5 day period, $\frac{0·73}{0·36}$ or 2·0 : 1.

When the bacterial numbers are examined, it is found that the oxidation processes taking place in the freshly synthesized diatom cultures were not accompanied by any appreciable increase of bacteria. To be sure, there were more bacteria in the bottles in which photosynthesis took place. Nevertheless, the bacterial population, as determined by the plate method, remained comparatively limited, even with the large amounts of fresh diatom material undergoing active oxidation in the dark. Those bacteria that were found in the bottles grew very slowly on the plates and required at least 7 days' incubation for an adequate count. One must, therefore, conclude that bacteria do not play any important role in the oxidation of fresh diatom material.

A microscopic examination of the plankton, centrifuged after varying periods of photosynthesis, revealed the presence of large numbers of diatoms, including species of *Nitzschia*, *Navicula*, *Rhizosolenia*, and others. However, after the diatoms had undergone oxidation in the dark following photosynthesis, microscopic examination of the centrifuged or sedimented material revealed

the presence of large numbers of Protozoa, especially certain types of amoebae, and ciliates, as well as flagellates, capable of feeding on diatoms. The bottles were also found to contain varying numbers of copepods. In the presence of such a large animal population, it seems highly probable that the effect of bacteria on the decomposition of the diatom constituents of the plankton was of minor importance. It is of interest to call attention to the suggestion of Lackey (1936) that Protozoa play an important role in the destruction of marine plant and animal residues, and also to the generally recognized role of the diatoms in the nutrition of copepods and other animal forms (Fuller & Clarke, 1936).

Discussion

The results obtained in these investigations point definitely to the fact that dead diatoms in sea water are rapidly decomposed by bacteria. In the absence of sufficient available energy, a part of the phosphate regenerated in the process of decomposition may be immediately liberated into the sea water whereas the rest, which represents the greater portion of the phosphate, is incorporated into the bacterial protoplasm as it is synthesized. Usually, however, there is an initial decrease of the dissolved phosphate due to its rapid consumption by the bacteria. The decomposition of the diatoms is accompanied by a marked increase in the bacterial population. The bacterial numbers reach a peak in a short time and then drop rapidly to low and fairly constant levels. With the death and autolysis of the bacteria, phosphate is again rapidly regenerated. Through the agency of this phosphorus cycle almost two-thirds of the phosphorus present in the dead diatoms was found in the sea water within 132 hours. In the presence of an adequate supply of available energy, all of the phosphate originally found in the sea water and also that amount which was liberated in the decomposition of the diatoms was consumed by the rapidly multiplying bacteria. But it in turn was soon regenerated into the sea water as the bacteria died and underwent autolysis.

Living diatoms, however, were not attacked by the bacterial population of the sea water. Although a greater bacterial population was usually found in the water containing living diatoms than in the untreated sea water, this increase is of a much smaller order of magnitude than that attained by bacteria in the presence of readily decomposable organic substances, as glucose or amino acids. Whereas in the breakdown of copepod plankton, a distinct parallelism was found between oxygen consumption, bacterial multiplication and ammonia liberation, in the case of the diatom plankton, no such parallelism existed. Nitrogen was liberated at a very slow rate, and the bacteria increased only to a limited extent, as compared with their numbers in the free water; this limited increase might have been due to the feeding of the bacteria on substances excreted by the diatoms or upon some of the dying diatoms.

Neither was the oxidation of freshly synthesized diatom material accompanied by active bacterial multiplication. The consumption of oxygen under

these conditions was due largely to the respiration of the diatoms themselves. It seems, therefore, that living diatoms, even when photosynthesis is excluded, possess considerable resistance to bacterial attack. They are gradually consumed, however, by the animal members of the plankton. This may further account for the fact that while the process of diatom breakdown is accompanied by oxygen consumption, it is not necessarily accompanied by a parallel increase in bacterial numbers.

The authors are indebted to Miss L. Lillick, for the identification of the diatoms, to Dr C. E. Renn, for assistance in the collection of the plankton, and to Dr M. Hotchkiss for assistance in the determination of bacterial numbers.

Summary

1. Dead marine diatom plankton was found to undergo rapid oxidation and decomposition when added to fresh sea water. This was measured by oxygen consumption, nitrogen liberation, phosphate regeneration and bacterial multiplication.

2. Living diatoms added to sea water and placed in the dark continued to absorb oxygen; they were rather resistant to bacterial attack.

3. Diatom-rich marine plankton also absorbed oxygen, while the phosphorus was gradually regenerated. The bacteria did not increase in numbers in correspondence with the oxidation of the fresh diatom material.

4. When sea water in which photosynthesis was allowed to proceed for varying periods of time was placed in the dark, rapid oxidation of the freshly synthesized material took place, as indicated by oxygen consumption and phosphate liberation. Although there was a greater number of bacteria in the water in which photosynthesis took place, the oxidation of the fresh diatom material was not accompanied by any large increase in bacteria; in fact a decrease in numbers was frequently observed.

5. When photosynthesis was stopped by placing the bottles in the dark, there was a marked increase in the numbers of Protozoa, notably various amoebae and ciliates, and also of copepods.

6. These results suggest that the animal forms may be largely responsible for the destruction of the living diatoms in the plankton. The role of bacteria in the regeneration of the nitrogen and phosphorus in the sea consists in the destruction of the dead diatoms as well as of the animal residues.

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Contribution No. 158

NOTE ON THE FLOW OF STREAMS IN A ROTATING SYSTEM

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Certain similarity of the observed flow in the ocean and in the atmosphere to the behavior of a wake stream, for which a complete, experimentally verified theory is available (*1*), led Rossby (*2*) to initiate the extension of the wake stream idea first to a rotating system and secondly, to a stratified medium. Several interesting predictions were made by Rossby as a result of his theoretical investigation; and it was the purpose of the experiments carried out by the author to investigate to what extent these predictions could be verified in the laboratory. The experiments were of an exploratory nature and the conclusions can in no way be regarded as final.

Preliminary tests were made in a small cylindrical tank subject to cyclonic rotation and with a jet so arranged that the influx of water took place radially from the periphery. With this system the path described by water injected through a point jet at the surface was demonstrated for various radii of the inertia circle and these flow patterns were compared with those obtained in the same fashion but with the jet extending the whole depth of the layer of water being investigated. In the latter case the flow patterns differed radically from the inertia circle, the anticyclones being very much larger for the deep jet than for the surface, point jet. This indicated that certain pressure gradients were established which served to balance to some extent the Coriolis' forces. That such pressure gradients will be established has been demonstrated mathematically by Taylor (*3*).

It was evident, however, that with the jet issuing from the side of the tank, the wall effect contributed to the balancing pressure gradients. To minimize this wall effect, therefore, a large tank 6 feet in diameter was constructed and the jet inflow arranged to take place radially outwards from the center. The water was brought to the tank from a stationary head cistern by means of a gland around the hollow axis of the tank and issued through a vertical slit in this hollow axis. In this system it was possible to vary the following parameters at will:—

(I) the depth, from 5 cm. to 40 cms.
(II) the head at the jet, from 10 cms. to 100 cms.
(III) the rotational speed, from 1¾ r.p.m. to 10 r.p.m.

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From Taylor's theory there is reason to expect, as indicated above, that the Coriolis or deflecting forces due to rotation would be completely balanced by pressure gradients resulting from the motion. Therefore, in a deep homogeneous medium with two dimensional motion, the flow pattern should be the same regardless of rotation and in the cylindrical tank described would take the form of a cyclone on the left side of the jet looking downstream and a symmetrically placed anticyclone on the right. Although Taylor's conditions were in no sense satisfied in the experimental arrangement described, they are approached more closely as the depth of the water in the tank increases, and therefore the flow patterns should show greater symmetry in the deeper cases. This was found to be the case; though, again, even in the deepest test made, the pressure gradients were far from completely balancing the deflecting force.

Rossby's extension of the wake stream theory to a rotating system calls for a counter-current on the left hand side of the jet, due to absorption there and ejection on the right side. This counter-current is brought about, in a homogeneous fluid, by deformations of the free surface and should be expected to be most marked for shallow depths. Thus it is seen that, whereas the counter-current does not appear to be compatible with the conception of completely balanced Coriolis forces, the two results are actually complementary cases at the extremes of the depth scale, viz.—in shallow layers the deformation of the free surface is percentually great compared to the depth and therefore the counter-current can be established, but in deep layers, where the surface deformations are percentually negligible, Taylor's reasoning applies.

This was well demonstrated in the six foot tank. With a head of 40 cms. and a rotation of 5 revolutions per minute, a clear counter-current accompanying a completely asymetrical flow pattern was observed for a depth of 6 cms., while for the same conditions of head and rotation, *i. e., the same radius of the inertia circle,* no counter-current and a markedly more symmetrical flow pattern was found when the depth was increased to 24 cms.

It has been pointed out that the effect of a given deformation of the free surface increases with diminishing depth, but decrease of depth also has the undesirable characteristic of accentuating the influence of bottom friction. The surface deformation effect can, however, be intensified, without decreasing the depth to the extent that bottom friction would play a noticeable role, by utilizing a stratified medium. Moreover, in nature, stratification often exists in the atmosphere and always is present in the ocean so that, while Taylor's conclusions are true for a homogeneous deep fluid, Rossby's speculations as to the motion in shallow depths and stratified media are the more significant in Meteorology and Oceanography by virtue of their closer relationship to the natural state.

In order to demonstrate this effect of stratification a rotating tank was

built having a four foot diameter and with 12 cms. depth; apart from its size this tank was similar in all respects to the larger one described above. Into the four foot tank was poured first a layer 6 cm. deep of a mixture, specific gravity 1.2, of Carbon Tetrachloride and Kerosene, and then above

KEY DIAGRAM

Figure 10. Surface flow in four foot rotating tank with stratification.

this the jet injected the wake stream into an overlying layer of water of equal depth. The water was allowed to overflow all around the edge of the tank, and when it is pointed out that the jet was only 12 thousandths of an inch wide it becomes evident that the distributed overflow would not

introduce any serious effect on the flow pattern. In the ideal case with this stratification, if the lower liquid were to rotate with the tank as a solid, deformations of the free water surface would be magnified at the internal boundary by a factor

$$\frac{\rho_{lower}}{\rho_{lower} - \rho_{upper}} = \frac{1.2}{0.2} = 6,$$

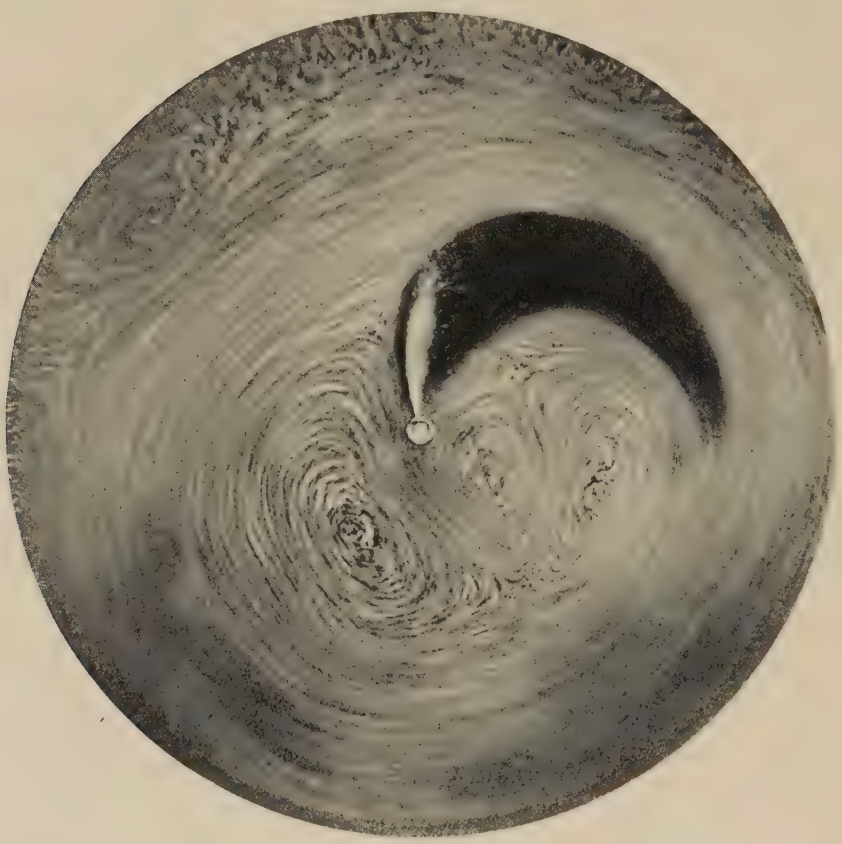

Figure 11. Surface flow in four foot rotating tank with stratification, ten revolutions per minute cyclonic rotation and 100 cms. head at jet.

and therefore the Rossby effects are magnified while the Taylor balance is diminished. In the practical experiment it is impossible to prevent the circulation of the water above from imparting a similar motion to the underlying denser liquid, and, hereby, a tendency to barotropy, which would

nullify the effectiveness of the stratification, occurs. Complete barotropy is prevented by bottom friction acting on the lower liquid and by the fact that the jet only plays in the overlying water and therefore a more intense counter-current and a less symmetrical flow is expected in the stratified than in the corresponding homogeneous case. Comparison of flow patterns for the two-layer and the homogeneous case shows this expectation to be justified.

In the case illustrated by the photograph reproduced here, chosen from an extensive series, the rotation was 10 revolutions per minute, the head 100 cms. and the two-layer stratification was employed. The flow may be easily traced by reference to the accompanying Key Diagram. Lycopodium powder was used as the indicating substance and the flow was photographed with the camera rotating with the tank. Examination of the pattern reveals that several of the features predicted are ratified to some extent at least in the experiment.

(I) A fully developed counter-current is established on the left hand side of the stream near the jet.

(II) Further downstream absorption on the left side is noticeable and such absorption implies the existence of a return current there also, but this counter-current is masked by the water sweeping around in the general anticyclonic motion and overlapping the wakestream.

(III) Ejection downstream on the right hand side is evident while on this side the only absorption noticeable occurs in the immediate proximity of the jet.

While these features to some extent are in accordance with Rossby's predictions it is also evident that important modifications to his analysis will have to made before the behavior of a wake stream in a rotating system can be completely explained.

It is interesting to note the flow at A and B in the photograph; the camera has caught two hyperbolic points in a classical pose.

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Contribution No. 164

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ON SECURING LARGE QUANTITIES OF DIATOMS FROM THE SEA FOR CHEMICAL ANALYSIS[1]

A KNOWLEDGE of the chemical composition of marine diatoms is desirable because of the essential role these organisms play each year in the constructive part of the food cycle of the sea and because of the importance diatom substance may have had in the formation of petroleum deposits. Although countless billions of diatoms may exist in small areas of the ocean, their minute size makes it extremely difficult to obtain any considerable quantity. Chief among the difficulties encountered are the very large volumes of water which must be strained and the rapid clogging of the filtering surfaces by the diatom cells. During the past summer at the Woods Hole Oceanographic Institution methods of circumventing these difficulties were explored.

The use of a large silk net towed from a boat was found more effective than the pumping method,[2] provided that the proper size mesh was selected for the type of diatoms desired. Another method, consisting of culturing a pure strain of diatoms on a large scale, is on trial by Mr. Bostwick Ketchum at the Harvard Biological Laboratories. However, exceedingly few species have been cultured successfully by any one. The advantages of procuring the diatoms directly from the sea are that any types occurring in great abundance (and hence important in the economy of the sea) can be obtained, that large quantities are procurable within a short time (at least six nets could be used simultaneously from a boat), and, since no danger exists of changes due to artificial conditions, the chemical constitution of the organisms secured will be as in nature.

[1] Contribution No. 164, Woods Hole Oceanographic Institution.

[2] However, pumps or sea-cocks have been found useful for collection of plankton in smaller quantities. *Cf.* L. D. Phifer, SCIENCE, 79: 298, 1934.

To permit any useful interpretation of the chemical analysis of the material obtained, a certain degree of purity of the catch is required. If particles of detritus or protozoans *of the same size* as the diatoms are abundant in the water, it is obviously impossible to obtain a large quantity of uncontaminated diatom material by simple straining. Another time or place must be sought. In cases in which the detritus is very finely divided, it can be avoided by the use of the coarsest net which will retain the diatoms. However, copepods or other crustacea are almost sure to be encountered, and, because of their larger size, even small numbers of these animals would be a serious contamination quantitatively. Success in excluding organisms larger than diatoms was attained through the use of a cone of coarser silk placed over the mouth of the net and towed apex foremost. The mesh of this cone was of such a size (No. 0 silk = 38 strands per inch) that the diatoms could pass freely through it, but copepods, etc., were stopped and swept off to one side.

Using one net (1 m diameter, 4 m long, No. 10 silk = 109 strands per inch) provided with a cone of this type, large quantities of diatoms were obtained on two occasions during September in Vineyard Sound. The net was towed at very slow speed, and at intervals of three minutes was hauled in and emptied. Each catch, which amounted to about six quarts of a thick suspension, was allowed to stand for two half-hour periods. At the end of each period the supernatant liquid, in which the diatoms remained suspended, was poured into a strainer, leaving in the bottom of each jar the heavier sand, detritus, and whatever zooplankton had accidentally entered. In the strainer (a bag of No. 20 silk) the material drained in the course of about half an hour to a sludge. For the first day's work, this sludge was spread out on towels to dry, and later transferred to a chemical hood heated to 40° C. On the second occasion the sludge was not dried but was shaken immediately with an equal volume of ether. As a result of a day's work we

obtained on the first occasion about 200 grams of dry, flaky material, and on the second occasion about two quarts of sludge in ether.

A complete analysis of the plankton in a sample of sea water taken during the first operation, kindly carried out for me by Miss Lois Lillick, showed that the concentration of diatoms in this area was almost 200,000 cells per liter. This approaches the maximum richness observed for diatom flowerings. One species of diatom (*Rhizosolenia alata*) composed 85 per cent. of the count, another species (*Corethron hystrix*) formed 8 per cent., and seventeen other forms together amounted to less than 7 per cent. Examination of a sample of the sludge indicated that the detritus and the animal contaminants were as low as ever found in phytoplankton hauls, in this case being certainly less than 1 per cent. of the total volume. All the material has been turned over to Professor Hans T. Clarke, of the Department of Biological Chemistry at Columbia University, for chemical analysis.

George L. Clarke

Biological Laboratories
Harvard University

Report of the year 1936

THE WOODS HOLE OCEANOGRAPHIC INSTITUTION

REPORT FOR THE YEAR 1936

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FRANK R. LILLIE, President of the Corporation, University of Chicago, Chicago, Ill.
LAWRASON RIGGS, JR., Treasurer, 120 Broadway, New York, N.Y.
HENRY B. BIGELOW, Clerk of the Corporation, Woods Hole, Mass.

II. MEMBERS OF THE CORPORATION

(As of December 31, 1936)

Charles Francis Adams, Boston, Mass.
Thomas Barbour, Museum of Comparative Zoölogy, Cambridge, Mass.
Henry B. Bigelow, Museum of Comparative Zoölogy, Cambridge, Mass.
Isaiah Bowman, Johns Hopkins University, Baltimore, Md.
The Commandant (Admiral R. R. Waesche), U. S. Coast Guard, for the time being, Washington, D.C.
E. G. Conklin, Princeton University, Princeton, N.J.
Benjamin M. Duggar, University of Wisconsin, Madison, Wis.
Marion Eppley, Newport, R.I.
John A. Fleming, Carnegie Institution, Washington, D.C.
Ross G. Harrison, Yale University, New Haven, Conn.
A. G. Huntsman, University of Toronto, Toronto, Canada
The Hydrographer (Capt. L. R. Leahy), U. S. Navy Department, for the time being, Washington, D.C.
Columbus O'D. Iselin, Woods Hole Oceanographic Institution, Woods Hole, Mass.
Frank B. Jewett, New York, N.Y.
Frank R. Lillie, University of Chicago, Chicago, Illinois
T. H. Morgan, California Institute of Technology, Pasadena, Calif.
R. S. Patton, U. S. Coast & Geodetic Survey, Washington, D.C.
Alfred C. Redfield, Harvard University, Cambridge, Mass.
Lawrason Riggs, Jr., New York, N.Y.
Elihu Root, Jr., New York, N.Y.
B. W. St. Clair, Cambridge, Mass.
Harlow Shapley, Harvard University, Cambridge, Mass.
Henry L. Shattuck, Boston, Mass.
T. Wayland Vaughan, Washington, D.C.

III. REPORT OF THE TREASURER

To the Members and Trustees:

Gentlemen:

At the meeting of the Trustees held last August, the fiscal year which formerly ended February 28th was changed to agree with the calendar year and it was voted that the report of the Treasurer cover the period March 1, 1936 to December 31, 1936. The accounts for this period have been audited by Messrs. Stagg, Mather & Hough, public accountants, and a copy of their report is on file in the office of the Institution.

During the period the proceeds from securities redeemed or sold was, $665,858.39. These were all bonds except one preferred stock (Standard Oil Export) and the annual income on these securities was, $29,205.00. The proceeds and in addition $7,961.08 was invested as follows:

In Bonds	$366,260.00	Fixed annual income	$14,312.50
Preferred stock	$122,891.50	Fixed annual income	5,947.50
Common stock	$184,667.97	Estimated ordinary income	8,945.00
		Total	$29,205.00

The return on the cost of the securities sold was .0443, on the value at time of sale or redemption, .0438 and on the new investments (ordinary dividends estimated) at cost .0390.

Due to the investment of the $7,961.00 (from amortization of premium and back dividends on preferred stock allocable to principal) in addition to the proceeds of sales and redemptions, the dollar income (with ordinary dividends estimated and special dividends excluded) remains the same.

A net profit of $6,793.64 was realized from the sale or redemption of securities to which must be added $2,398.60 being reserve for amortization of premiums applicable to securities disposed of, making $9,192.24. At the beginning of the period there were unamortized losses on securities sold of $4,696.05. Applying the above gains for the period leaves a net realized gain in endowment account of $4,496.19.

Extra dividends and special dividends on stock amounting to $8,224.25 were placed in a Special Income Account.

A payment of $2,366.27 was received from the Rockefeller Foundation. This was made so as to bring the total of income for the year ending February 29th, 1936, when the annual grant was capitalized, up to the income for the prior year. With this payment the Rockefeller Foundation has completed all its obligations to the Institution.

The following are summaries of the various accounts:

		BALANCE
ENDOWMENT FUND ASSETS		
Investments, at cost:		
Endowment Fund bonds	$1,509,529.20	
(Market Value $1,574,191.25)		
Endowment Fund stocks	$ 908,030.96	
(Market Value $1,035,192.00)		
Reserve Fund bonds	$ 3,970.00	
(Market value $3,705.00)		
Reserve Fund stocks	$ 25,723.99	
(Market value $19,500.93)		
		$2,447,254.15
Cash:		
Endowment Fund:		
In Bank	$ 12,677.03	
Reserve Fund	2,299.66	14,976.69
		$2,462,230.84
PLANT ASSETS		
Laboratory plant:		
Land	$ 27,072.32	
Building	323,213.12	
Laboratory equipment	21,361.93	
Crew room equipment	557.95	
Library	9,500.00	
		$381,705.32
Ship "Atlantis"		
Construction	$218,674.47	
Equipment	27,298.50	
		245,972.97
Small boat and equipment		$ 6,570.55
Depreciation Fund (reserve for periodical replacements)		
Investments—Bonds	$ 7,000.00	
(Market value $7,251.56)		
Cash	$ 16,170.16	
		23,170.16
		$657,419.00
CURRENT ASSETS		
Cash—Current funds	$11,539.52	
Cash—Special Income Account	8,224.25	
		$19,763.77
Interest receivable		
(Accrued interest paid on bonds purchased)		504.67
		$20,268.44

SHEET

ENDOWMENT FUNDS

Endowment Fund—General		$2,000,000.00	
Endowment fund for upkeep of plant		419,419.96	
		$2,419,419.96	
Add:			
Realized net gain on securities called or sold	$4,496.19		
Reserve for amortization of bond premiums	6,321.04	10,817.23	
			$2,430,237.19
Reserve fund			31,993.65
			$2,462,230.84

PLANT FUNDS

Plant fund—General	$607,642.13
Plant fund from current account	26,606.71
Reserve for depreciation (Reserve for periodical replacements)	23,170.16
	$657,419.00

CURRENT LIABILITIES AND SURPLUS

Accounts payable		$ 3,235.76	
Bank overdraft		35.17	
			$ 3,270.93
Current surplus and reserve for "working balance":			
Reserve for working balance		$ 5,000.00	
Current surplus—Balance at February 29, 1936	$3,045.17		
Excess of income over expenditures, for the period ended December 31, 1936	8,952.34	11,997.51	16,997.51
			$20,268.44

GENERAL ACCOUNT

Income:			
Income from endowment funds:			
Interest	$52,196.44		
Dividends (including extra dividends of $8,224.25)	44,918.87		
		$97,115.31	
Less—Custodian Fees		1,331.52	
		$95,783.79	
Appropriation from Rockefeller Foundation for current expenses		$ 2,366.27	$98,150.06
Expenses:			
Upkeep of Plant:			
Upkeep of buildings and grounds		$ 5,532.18	
Upkeep of *Atlantis*		8,199.93	
Upkeep of *Asterias*		63.79	
Insurance		5,444.00	
Reserve for depreciation		4,000.00	
		$23,239.90	
Operating Expenses:			
Operation of *Atlantis*	$24,560.90		
Operation of *Asterias*	804.95		
Scientific salaries	22,514.50		
Scientific supplies & equipment	3,713.04		
Travelling expenses	643.98		
Publications	2,943.23		
Administration	5,966.46		
Amortization of bond premiums	2,743.20		
Contribution to retirement fund	1,567.56	65,457.82	
		$88,697.72	
Expenditures for permanent plant additions:			
Additions to library		$ 500.00	$89,197.72
Excess of income over expenditures			$ 8,952.34

Due to the number of securities that have been called the duties of the Finance Committee have again been exceptionally heavy and the Treasurer wishes to acknowledge their invaluable services.

RETIREMENT FUND

There was in the Retirement Fund at the end of the year the sum of $9,479.56 represented as credits on the bank books held by the Institution for the participants numbering 20.

Respectfully submitted,

LAWRASON RIGGS, JR.,
Treasurer

March 25, 1937

IV. SEVENTH ANNUAL REPORT OF THE DIRECTOR FOR THE YEAR 1936

BY HENRY B. BIGELOW

Equipment

The chief mechanical improvement made in the laboratory building during the past year has been the reconstruction of the CO_2 refrigeration system in the basement, which is designed to deliver cooled water to the aquarium room. In the original installation, sea water from the storage tanks in the attic was cooled by passage through a coil immersed in a tank of brine which was in turn chilled to a low temperature by CO_2 coils operated by a condenser of the sort usual in this type of refrigeration. It proved, however, that the amount of water that could be chilled in this was not sufficient for our purposes. In the new arrangement, the cool brine is pumped through coils installed in the aquarium tanks, so that the latter are chilled direct.

We have to thank Mr. G. K. Saurwein of the Harvard Maintenance Department for designing the new set-up.

A device has also been perfected for warming cold water, which consists of a lead coil run through a sand bath, heated by a small flame.

The only new scientific equipment deserving of comment, aside from ordinary replacements, is the adaptation of a current meter for use in a frame resting on the sea bottom, making it possible to make direct measurement of currents close to the sea floor, a long-felt want.

No important reconstruction of scientific equipment has been found necessary on "Atlantis." As in the past, all routine maintenance, aside from docking and machine work needed in the engine room, has been carried out by our own crew. While the ship was laid up during January and February, four of the water tanks were moved and the skin of the ship behind them was coated with bitumastic to guard against corrosion. When the ship was in the shipyard, manholes were cut in the main deck of the mess room, making it possible to do the same work in the case of the two remaining water tanks. The mizzen standing rigging has been replaced, and next year we contemplate replacing the main rigging.

While the ship was in port during November and December, the sheathing in two of the staterooms was removed, the inside of the hull covered with bitumastic, and the sheathing replaced and

painted. One more water tank was overhauled. A new galley range was installed, and the batteries were tested and found to be in good condition.

"Asterias" has required only routine maintenance. Both vessels are in better condition now than at any time since they were built.

Since purchase of the two whaleboats mentioned in my last report, we have had little use for the dories formerly carried by "Atlantis." One of these was sold.

There have been no accidents to either vessel.

An inspection of the piles of the dock, and of the float by T. N. Kelley, first officer of "Atlantis," has shown that piles, cribbings and tie planks were sound on all sides with no soft spots indicating worm-action, while nuts and bolts show but little rust. That no sign of damage was found after five years' submersion bears witness to the efficiency of the treatment the lumber received.

Loans

Various articles of scientific equipment have been loaned us by Brown University, and by the Biological Laboratories and Fatigue Laboratory of Harvard University.

On the other hand, we have loaned two Greene-Bigelow water bottles and two deep sea reversing thermometers to the Chesapeake Biological Laboratory; also a set of Knudsen hydrometers to the Massachusetts Institute of Technology.

Acknowledgments

A beautiful carved walnut bookcase for the ward room on "Atlantis" was presented by Mrs. Alfred C. Potter in memory of her son, Delano Potter, formerly second officer, whose tragic death is referred to in my last report.

We also owe thanks to the U. S. Hydrographic Office and to the U. S. Coast and Geodetic Survey for their continued generosity in supplying us with charts.

Library

Our contribution to the library of the Marine Biological Laboratory was reduced this year from $1000 to $600 which is little more than is needed to maintain subscriptions to current serials. Eleven books, and four back sets were purchased, subscriptions to 37 current journals were continued, and 196 volumes were bound.

Titles received by gift or by exchange during the past year number about 350.

Personnel

Commander Edward H. Smith, who has worked at the laboratory during the past three years in connection with the oceanographic investigations of the Ice Patrol, was ordered to San Francisco in June to take command of the Coast Guard Cutter "Tahoe."

Mr. Columbus O'D. Iselin, in addition to his work with us, was appointed Lecturer in Oceanography at Massachusetts Institute of Technology, and delivered a series of lectures there.

Dr. Charles E. Renn now holds an appointment as tutor and instructor in Harvard University in addition to his appointment on our staff and his salary is divided between the two institutions.

The following Fellowship holders worked at Woods Hole during the summer:

Margaret Butler, A. E. Cooper, Victor Emmel, Margaret Hotchkiss, Sidney C. T. Hsiao, Bostwick H. Ketchum, Frederick K. Sparrow, Jr., Robert C. Stauffer, Th. von Brand, Lionel A. Walford, Wm. F. Wrath.

One appointee, W. H. Johnson, whose studies required work in more northern waters, worked at the Atlantic Biological Station at St. Andrews, New Brunswick.

The following visiting investigators have been at the Institution since the last report: Dr. Edgar Allen, Dr. Joseph A. Cushman, Dr. R. G. Gould, Benjamin B. Leavitt, Raymond B. Montgomery, Dr. G. H. Parker, Dr. Charles Piggot, I. I. Schell, Comdr. E. H. Smith, Dr. C. B. Wilson, Dr. C. P. Winsor, Donald J. Zinn.

In July we had a short visit from Dr. H. U. Sverdrup of the Geophysical Institute of Bergen who is assuming the directorship of the Scripps Institution of Oceanography succeeding Dr. T. W. Vaughan. Professor Johan Hjort of the University of Oslo also visited the laboratory in August and September. He brought with him Captain Hagbart Hoium, an expert shrimp fisherman, also a set of gear. And, on a cruise of "Atlantis," successful trawling was carried out for shrimps in the Gulf of Maine, giving promise of future commercial development.

There have been one technician, and 21 assistants to members of the staff, 8 of whom either worked as volunteers or were paid from other sources.

Thirty institutions have been represented this year in the laboratory or on "Atlantis" cruises as follows: Barnard College; Berkshire School; Brown University; Carnegie Institution; Dalhousie University; Dartmouth College; Flower Medical School; Geophysical Insti-

tute, Bergen, Norway; Harvard University; Johns Hopkins University; International Ice Patrol; Massachusetts Institute of Technology; Queen's University; Radcliffe College; Rutgers University; Sarah Lawrence College; State Teachers College; University of Illinois; University of Iowa; University of Michigan; University of Oslo; U. S. Bureau of Fisheries; U. S. Coast Guard; U. S. Weather Bureau; Yale University.

During the year 38 scientists have gone out on "Atlantis." Eighty-eight persons of all categories have worked at the Institution during the past year.

There has been no change among the officers of "Atlantis." Captain G. W. Carlson has continued in charge of "Asterias," assisted by Charles Butcher II, Harlan Hyde and Matthew Pratt.

The only accident was a dislocated shoulder suffered by Ernest Siversen, on "Atlantis." After treatment, he was able to return to duty.

Foreign Travel by the Staff

Dr. George L. Clarke was in Europe from April until July, first in attendance at the annual meeting of the International Council for the Exploration of the Sea at Copenhagen and subsequently visiting a number of oceanographic laboratories.

Prof. C.-G. Rossby attended the meeting of the International Geophysical Union in Edinburgh, and likewise visited the Central Geophysical Observatory in Leningrad.

Mr. Columbus O'D. Iselin went to the meeting of the International Geophysical Union in Edinburgh, and in London represented the Institution at conferences concerning the proposed joint program of Woods Hole Oceanographic Institution and the Bermuda Biological Station. In Copenhagen, he visited Burmeister & Wain to discuss repairs to "Atlantis" fuel pumps.

Publication

Three numbers of "Papers in Physical Oceanography and Meteorology" appeared, Volume IV, numbers 3 and 4 and Volume V, number 1.

The following contributions were published between January 1, 1936 and December 31, 1936:

No. 65. Lackey, James B. Occurrence and Distribution of the Marine Protozoan Species in the Woods Hole Area. Biol. Bull. Vol. LXX, No. 2, pp. 264–278. 1936.

No. 78. Waksman, Selman A. and Charles E. Renn. Decomposition of Organic Matter in Sea Water by Bacteria. III. Factors Influencing the Rate of Decomposition. Biol. Bull. Vol. LXX, No. 3, pp. 472–483. 1936.

No. 80. Stetson, Henry C. Geology and Paleontology of the Georges Bank Canyons. I. Geology. Bull. Geol. Soc. America, Vol. 47, pp. 339–366. 1936.

No. 81. Stephenson, Lloyd William. Geology and Paleontology of the Georges Bank Canyons. II. Upper Cretaceous Fossils from Georges Bank (Including Species from Banquereau, Nova Scotia). Bull. Geol. Soc. America, Vol. 47, pp. 367–410. 1936.

No. 82. Cushman, Joseph A. Geology and Paleontology of the Georges Bank Canyons. IV. Cretaceous and Late Tertiary Foraminifera. Bull. Geol. Soc. America, Vol. 47, pp. 413–440. 1936.

No. 83. Wald, George. Pigments of the Retina. II. Sea Robin, Sea Bass, and Scup. Jour. Gen. Physiol., Vol. 20, No. 1, pp. 45–56. 1936.

No. 84. Bassler, R. S. Geology and Paleontology of the Georges Bank Canyons. III. Cretaceous Bryozoan from Georges Bank. Bull. Geol. Soc. America, Vol. 47, pp. 411–412. 1936.

No. 85. Fish, Charles J. The Biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. Biol. Bull. Vol. LXX, No. 1, pp. 118–141. 1936.

No. 86. Rakestraw, Norris W., Henry E. Mahncke and Eliot F. Beach. Determination of Iron in Sea Water. Analyt. Ed. Ind. and Eng. Chemistry, Vol. 8, p. 136. 1936.

No. 88. Watson, E. E. Mixing and Residual Currents in Tidal Waters as Illustrated in the Bay of Fundy. J. Biol. Bd. Can. 2 (2), pp. 141–208. 1936.

No. 90. Renn, Charles E. The Wasting Disease of *Zostera marina*. I. A Phytological Investigation of the Diseased Plant. Biol. Bull., Vol. LXX, No. 1, pp. 148–158. 1936.

No. 92. Fuller, John L. and George L. Clarke. Further Experiments on the Feeding of *Calanus finmarchicus*. Biol. Bull., Vol. LXX, No. 2, pp. 308–320. 1936.

No. 94. Fish, Charles J. The Biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXX, No. 2, pp. 193–216. 1936.

No. 95. Johnson, Frank H. The Oxygen Uptake of Marine Bacteria. Jour. Bacteriology, Vol. 31, No. 5, pp. 547–556. 1936.

No. 96. Graham, Michael. Investigations of the Herring of Passamaquoddy and Adjacent Regions. J. Biol. Bd. Can. 2 (2), pp. 95–140. 1936.

No. 98. Powell, Wilson M. and George L. Clarke. The Reflection and Absorption of Daylight at the Surface of the Ocean. Jour. Op. Soc. Amer., Vol. 26, pp. 1–23. 1936.

No. 99. Sparrow, F. K., Jr. Biological Observations on the Marine Fungi of Woods Hole Waters. Biol. Bull., Vol. LXX, No. 2, pp. 236–263. 1936.

No. 100. Clarke, George L. On the Depth at which Fish can see. Ecology, Vol. 17, No. 3, pp. 452–456. 1936.

No. 101. Clarke, George L. Light Penetration in the Western North Atlantic and its Application to Biological Problems. Rapp. et Proc. Verb. Cons. Perm. Internat. Exp. Mer., Vol. 101, Part 2, pp. 1–14. 1936.

No. 102. Rossby, C.-G. and R. B. Montgomery. I. On the Frictional Force between Air and Water and on the Occurrence of a Laminar Boundary Layer next to the Surface of the Sea. C.-G. Rossby. II. Measurements of Vertical Gradient of Wind over Water. R. B. Montgomery. III. Transport of Surface Water due to the Wind System over the North Atlantic. R. B. Montgomery. Papers in Physical Oceanography and Meteorology, Vol. 4, No. 3, pp. 1–101. 1936.

No. 103. Stetson, H. C. Dredge-Samples from the Submarine Canyons between the Hudson Gorge and Chesapeake Bay. Trans. Am. Geophys. Union, Seventeenth Ann. Meeting, pp. 223–225. 1936.

No. 104. Iselin, Columbus. The Influence of the Mediterranean Outflow at Mid-Depths in the Sargasso Sea. Trans. Am. Geophys. Union, Seventeenth Ann. Meeting, pp. 219–221. 1936.

No. 105. Montgomery, R. B. Computation of the Transport of Surface-Water due to the Wind-System over the North Atlantic. Trans. Am. Geophys. Union, pp. 225–229. 1936.

No. 106. Hotchkiss, Margaret and Selman A. Waksman. Correlative Studies of Microscopic and Plate Methods for Evaluating the Bacterial Population of the Sea. Jour. Bacteriology, Vol. 32, No. 4, pp. 423–432. 1936.

No. 108. Iselin, Columbus. Study of the Circulation of the North Atlantic Ocean. Papers in Physical Oceanography and Meteorology, Vol. 4, No. 4, pp. 1–101. 1936.

No. 109. Fish, Charles J. The Biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXXI, No. 1, pp. 168–187. 1936.

No. 110. Rakestraw, Norris W. The Occurrence and Significance of Nitrite in the Sea. Biol. Bull., Vol. LXXI, No. 1, pp. 133–167. 1936.

No. 113. Parker, G. H. The Reactivation by Cutting of Severed Melanophore Nerves in the Dogfish Mustelus. Biol. Bull., Vol. LXXI, No. 2, pp. 255–258. 1936.

No. 114. Mitchell, Philip H., Kurt Buch and Norris W. Rakestraw. The Effect of Salinity and Temperature upon the Dissociation of Cresol Red and Phenol Red in Sea Water. Jour. du Conseil, Vol. XI, No. 2, pp. 183–189. 1936.

No. 115. Rossby, C.-G. Dynamics of Steady Ocean Currents in the Light of Experimental Fluid Mechanics. Papers in Physical Oceanography and Meteorology, Vol. 5, No. 1, pp. 1–43. 1936.

No. 116. Winsor, Charles P. and Lionel A. Walford. Sampling Variations in the Use of Plankton Nets. Jour. du Conseil, Vol. XI, No. 2, pp. 190–204. 1936.

No. 117. Renn, Charles E. Persistence of the Eel-Grass Disease and Parasite on the American Atlantic Coast. Nature, Vol. 138, p. 507. 1936.

No. 119. Bigelow, Henry B. and William C. Schroeder. Supplemental Notes on Fishes of the Gulf of Maine. Bull. Bur. Fisheries, Vol. XLVIII, Bull. No. 20, pp. 319–343. 1936.

No. 120. Rakestraw, Norris W. and Alexander Hollaender. Photochemical Oxidation of Ammonia in Sea Water. Science, Vol. 84, No. 2185, pp. 442–443. 1936.

No. 122. Redfield, Alfred C. An Ecological Aspect of the Gulf Stream. Nature, Vol. 138, p. 1013. 1936.

No. 128. Wrath, William F. Contamination and Compaction in Core Sampling. Science, Vol. 84, No. 2189, pp. 537–538. 1936.

The fourth volume of "Collected Reprints" (1935) was distributed in March. "Atlantis" station data were forwarded to the International Council for the Exploration of the Sea for publication in the Bulletin Hydrographique and the volume for 1935 has appeared.

Coöperation

Coöperation with the International Ice Patrol Service operated by the U. S. Coast Guard and with the U. S. Coast and Geodetic

Survey has continued along the lines described in my last report.

During April, "Atlantis" was sent to Georges Bank on a trawling trip for the Bureau of Fisheries in connection with haddock investigation, with Mr. W. C. Herrington of the Bureau as scientist in charge. The Bureau contributed toward the expense incurred.

In October, Mr. Henry Stetson and Dr. C. S. Piggot of the Geophysical Laboratory in Washington, took a series of cores down the continental slope south of Martha's Vineyard from the 100 fathom curve nearly to 2000, using the improved coring tube designed by Dr. Piggot.

"Atlantis" was not sent to the Gulf of Mexico the past winter for it seemed necessary that Professor Parr work up the data already at hand.

However, such a cruise is planned for the coming winter under the same coöperative arrangement with Bingham Oceanographic Foundation, as in the winters of 1933 and 1934 (see earlier reports), and "Atlantis" sailed southward on December 27.

A program of joint investigation with the Bermuda Biological Station into the variation of the North Atlantic drift has been considered during the past year. On December 26th the Trustees of the Bermuda Biological Station received word from England that the grant of money from the Empire Development Board had been approved by the Treasury officials, and that a committee of the Royal Society had been appointed to administer the funds. This coöperative undertaking holds great promise and the preliminary program is being gradually developed to include both physical and biological studies.

Field Work

Operations of "Atlantis" for the year are as follows:

Cruise 53: February–April; Eastern Slope Water Survey.
Cruise 54: April–May; Georges Bank.
Cruise 55: May; Gulf of Maine.
Cruise 56: June; Eastern Slope Water Survey.
Cruise 57: July; South of the Gulf Stream.
Cruise 58: July; Georges Bank.
Cruise 59: August; South Channel.
Cruise 60: August; Off Montauk and Gulf of Maine.
Cruise 61: August; Gulf of Maine.
Cruise 62: August-September; South to Slope Water.
Cruise 63: September–October; Eastern Slope Water Survey.
Cruise 64: South of Nantucket Shoal Lightship.

Summary of observations

Total distance sailed, miles	14,229
Number of days at sea	163
Deep stations	147
Shallow stations	59
Trawling stations	132
Temperature-Salinity and Oxygen	3,850
Other chemical determinations	675
Tows with closing nets	18
Bottom dredge samples and mud cores	48
Bottom current measurements	13

"Asterias" was kept in commission throughout the winter, to make monthly collecting trips to the offing of Gay Head in connection with Dr. Clarke's investigations of the seasonal production of Calanus. During the summer, she continued to serve the need of various investigators on short trips, partly collecting data, and partly in connection with the development of new gear.

Staff Meetings

Staff meetings were held weekly during the summer, in which the following speakers participated: Dr. Margaret Butler, Prof. Johan Hjort, Columbus Iselin, Dr. Norris W. Rakestraw, Dr. Charles E. Renn, Prof. C.-G. Rossby, Henry C. Stetson, Dr. H. U. Sverdrup, Dr. Th. v. Brand, Dr. Selman A. Waksman, Dr. Lionel A. Walford and Dr. C. P. Winsor.

V. STAFF

(As of December 31, 1936)

Henry B. Bigelow, Professor of Zoölogy, Harvard University, Director
Cornelia L. Carey, Barnard College, Research Associate in Marine Bacteriology
George L. Clarke, Tutor and Instructor, Harvard University, Junior Biologist
Columbus Iselin, Assistant Curator of Oceanography, Museum of Comparative Zoölogy, Research Associate in Physical Oceanography
A. E. Parr, Curator of the Bingham Oceanographic Collection, Yale University, Research Associate in Oceanography
Norris W. Rakestraw, Associate Professor of Chemistry, Brown University, Research Associate in Physical Chemistry
Alfred C. Redfield, Professor of Physiology, Harvard University, Senior Biologist
C. E. Renn, Tutor and Instructor, Harvard University, Junior Marine Bacteriologist
C.-G. Rossby, Professor of Meteorology, Massachusetts Institute of Technology, Oceanographer
H. R. Seiwell, Investigator in Oceanography
Floyd M. Soule, Senior Physical Oceanographer, U. S. Coast Guard, Research Associate in Oceanography
Henry C. Stetson, Assistant Curator in Paleontology, Museum of Comparative Zoölogy, Research Associate in Submarine Geology
Selman A. Waksman, Microbiologist, New Jersey Agricultural Experiment Station, Marine Bacteriologist
E. E. Watson, Assistant Professor of Physics, Queen's University, Research Associate in Physical Oceanography
Captain Sir Hubert Wilkins, Honorary Research Associate in Oceanography

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William C. Schroeder, Business Manager
Miss Virginia B. Walker, Secretary and Administrative Assistant
William Schroeder, Superintendent of Buildings and Grounds

APPENDIX

Reports of progress by investigators working at the Institution during 1936.

EFFECT OF TEMPERATURE ON GROWTH OF COD, AND OF THEIR SCALES

HENRY B. BIGELOW AND WILLIAM C. SCHROEDER

The experiment begun in 1935 was continued. But difficulty was experienced in obtaining small fish, and it was well into the summer before the refrigeration system was finally adjusted.

ZOÖPLANKTON STUDIES

HENRY B. BIGELOW AND MARY SEARS

1. Study was continued of Bermudian medusae collected by Dr. William Beebe, 1929–1930.

2. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. Zoöplankton. Progress has been made on analysis of the data, and on preparation of the final report.

3. Siphonophorae of the "Thor" Expedition, 1908-1910, to the Mediterranean. The report was completed and the first proof returned to the printer.

SEASONAL PRODUCTION OF PLANKTON, FEEDING OF COPEPODS, AND PENETRATION OF LIGHT INTO THE SEA

GEORGE L. CLARKE

1. The investigation of the seasonal production of plankton at the station off No Man's Land was continued until the middle of September (with the assistance of Mr. D. J. Zinn), thus completing a series of observations extending over fifteen months. From the collections of zoöplankton, phytoplankton, and nannoplankton, and from the records of temperature, salinity, phosphates, nitrates, and illumination, a study is now being made of the seasonal changes in the plankton and of the factors which control growth, breeding, etc. The annual production of the copepod, *Calanus finmarchicus* has already been worked out and the existence of two distinct breeding periods has been demonstrated. The measurements of light penetration reveal rather profound seasonal changes in the transparency of the water.

The seasonal changes in the bacterial population at this station have been studied by Dr. C. E. Renn, and the phytoplankton catches are being carefully analyzed by Miss Lois Lillick. Dr. John Fuller also collaborated with further experiments in the laboratory on the feeding rate of *Calanus*.

2. At the meeting of the International Council for the Exploration of the Sea at Copenhagen in May, a paper was presented on "Light Penetration in the Western North Atlantic and its Application to Biological Problems."

STUDIES OF THE FORAMINIFERA OCCURRING UNDER VARIOUS BOTTOM CONDITIONS IN THE WOODS HOLE REGION

J. A. CUSHMAN

Samples from Vineyard Sound and Buzzards Bay were taken and their foraminiferal content studied. Bottom conditions in Vineyard Sound have changed decidedly since the Biological Survey was made by the U. S. Bureau of Fisheries in 1904 and 1905. Numerous additions to the known fauna of the region were found.

FEEDING RATE OF CALANUS FINMARCHICUS IN RELATION TO ENVIRONMENTAL CONDITIONS

JOHN L. FULLER

The study of the nutritional physiology of *Calanus* was carried forward on two main fronts during the summer. (1) Measurements were made of the rate of capture of the diatom, *Nitzschia closterium*, under various conditions of light, temperature and diatom concentration. (2) An attempt was made to determine the minimum food requirement of this copepod by feeding it on various dilutions of diatoms.

It was found that under similar conditions the rate of capture of the diatoms was proportional to their concentration. In other words, *Calanus* does not speed up its feeding activity when food is scarce. There was some indication of a diurnal feeding rhythm with more activity at night, and feeding was found to be more rapid at 8° C. than at 3° or 13°.

It is impossible at present to state definitely the minimum food requirement of *Calanus*, but indications are that it is less than has

been estimated from measurements of oxygen consumption. Growth is somewhat more rapid with increased food supply, but results are variable.

The laboratory program has been supplemented by field studies on the amount of particulate organic matter present in Vineyard Sound where *Calanus* was collected throughout the summer. Through the kindness of Dr. von Brand it was possible to compare the organic nitrogen content of the *Nitzschia* used in the experiments, with that of the particulate matter in Vineyard Sound. The results of this comparison and of the other laboratory work are consistent with the ecological relations of *Calanus* insofar as they are known.

PHYSICAL OCEANOGRAPHY

COLUMBUS ISELIN

During last winter considerable time was devoted to assisting Prof. Rossby in a course of lectures on physical oceanography at the Massachusetts Institute of Technology. Since the month of June was spent at sea on the "Atlantis," it was not until August that the manuscript of a paper on the circulation of the Western North Atlantic was finally ready for the printer. In September I attended the sixth general Assembly of the International Union of Geodesy and Geophysics at Edinburgh. Since returning to Woods Hole, my time has been divided between getting the "Atlantis" ready for the winter cruise and a preliminary study of the data collected during three surveys of the eastern slope water area.

Because Mr. Woodcock has had to spend a large part of his time at sea, the correction of temperature observations and the analysis of salinity samples has fallen slightly behind. At the end of the year there remain about 900 water samples unattended to. However, he has found time during the autumn to put the laboratories and apparatus aboard the "Atlantis" in first-class condition.

Two plans of international coöperation in physical oceanography have gradually developed during the past year. An intensive survey of the area between the Grand Banks and Europe with at least six ships taking part has been tentatively set for the summer of 1938. Even more satisfactory are the arrangements which have been concluded between the Bermuda Biological Station and a special committee of the Royal Society of London. In coöperation with the Woods Hole Oceanographic Institution, it has been decided to begin at once a five year program of investigation on the fluctuations in the warm currents of the North Atlantic.

THE EFFECT OF LIGHT ON THE HERRING AND ITS FOOD

W. H. JOHNSON

Investigations were carried out during the past summer to determine the rôle played by light in determining the copepods chosen as food by the herring of Passamaquoddy Bay.

In localities devoid of strong tidal currents, the vertical distribution of the common copepods was determined both during a period of 24 consecutive hours and on separate occasions. Collections were made at four different depths under any one condition of light, the intensity of which was measured, whenever possible, by means of a photometer. Measurements were also made of the transparency of the water. Collections were subsequently analyzed into species, sex, and state of maturity.

Records of the vertical distribution of the herring under different conditions of light were made by (a) using a hydro-periscope capable of giving a view horizontally down to a depth of ten feet (b) setting three gill nets one below the other (c) dropping a small lead weight suspended at the end of a black thread among a school of herring and feeling the resulting vibrations (d) estimate when seen swimming.

Herring stomachs were analyzed to determine both when and what the fish eat under different conditions of light.

INVESTIGATIONS OF BATHYPELAGIC ZOÖPLANKTON

BENJAMIN B. LEAVITT

Collections of bathypelagic zoöplankton collected by means of closing nets during the previous three summers were studied statistically in the laboratory. The volumes of plankton caught at depths two hundred meters apart, collected at ten stations, in 117 hauls, reveals that there is a minimum quantity of animals at a depth of approximately 1200 m. There is also at least one level below this minimum which is considerably richer in material.

The animals were sorted into groups: Copepods, Schizopods, Decapods, Coelenterates, Chaetognaths, Fish, and Residue. These groups were measured and vertical distribution curves plotted for each group at each station for comparison with similar curves for the total volumes.

The Euphausiids from each haul were identified and counted in order that the vertical and horizontal distribution of that group might be better understood.

Comparisons were made between the vertical distribution of quantities of plankton and the temperature, salinity, and density of the water.

COLOR CHANGES OF ELASMOBRANCH FISHES

G. H. PARKER

Work was carried on, from May to September, on the color changes of young smooth dogfishes and mature individuals of the same species. Young dogfishes change from light to dark within a half hour after their birth and show all the characteristic peculiarities of the adult fishes. In this respect they are wholly unlike teleosts, which usually are hatched with a very imperfect color system, and in many cases are quite incapable of the characteristic adult changes which come on only after several days.

Studies on the adult dogfishes showed that their color changes, nervous in character, were induced by a substance given out from the nerves, which on chemical examination, proves to be very like sterol. This is a novel discovery for thus far sterols and like chemical materials have never been associated with color changes. A paper on the immature changes has already been published in the Biological Bulletin. The report on the adult fishes is in press.

INVESTIGATIONS IN COÖPERATION WITH THE BINGHAM OCEANOGRAPHIC FOUNDATION OF YALE UNIVERSITY

A. E. PARR

Since no joint cruises were made in 1936, work on the coöperative projects was limited to a continued analysis and preparation of reports on the data and material gathered during the preceding years. Through this respite from field work, which had become quite essential at this time by the vast accumulation of observations, it became possible to make considerable progress towards bringing the analyzed results and final conclusions up-to-date in manuscript or published form.

The critical examination of the large collection of floating sargassum weeds has been almost completed, and a first report on the quantitative and general ecological results will be ready for publication at an early date. Mr. Burkenroad's investigation of the ecology of the associated animal life has reached a similar stage and will be ready to appear in conjunction with a report on the weeds themselves.

A first report on the hydrographic observations made during 1933 and 1934 in the Caribbean area has appeared in print (A. E. Parr: A Contribution to the Hydrography of the Caribbean and Cayman Seas. Bull. Bingham Oceanog. Coll., Vol. V, Art. 4, Jan. 1937). A general theoretical principle concerning the inverse relationship between horizontal and vertical stability has also been suggested and separately published (A. E. Parr: Journal du Conseil, Dec. 1936) with the hydrographic observations from the eastern Caribbean serving as an example of unusual value for the investigation of this particular problem as it involves the relationship between ocean currents.

Good progress has also been made in the study of the deep-sea fishes (Sears and Parr) and the deep-sea shrimps (Burkenroad) collected by the "Atlantis" during previous joint cruises.

CHEMISTRY OF SEA WATER

NORRIS W. RAKESTRAW

The details of a new method for the determination of gaseous dissolved nitrogen in sea water have been satisfactorily worked out and a few actual determinations made. This has been largely the work of Mr. Victor Emmel. Since the procedure cannot well be carried out on shipboard, a method has been perfected for sealing up water samples in citrate bottles without any air present, so that analysis may be made on return to the laboratory. It is hoped that within another season the analytical method may be extended to include dissolved argon.

With the coöperation of Drs. von Brand and Renn, and Mr. Hurdis, study was made of the experimental decomposition and regeneration of nitrogenous organic matter in sea water. A paper embodying these results is being published, and it is planned to continue this study further in view of their interesting implications.

A short paper has been published (in coöperation with Dr. Alexander Hollaender) on the photochemical oxidation of ammonia in sea water, by means of ultraviolet radiation.

PHYSIOLOGY OF MARINE ORGANISMS AND BIOLOGY AND CHEMISTRY OF THE GULF OF MAINE

ALFRED C. REDFIELD

The analysis of material collected during the systematic survey of the Gulf of Maine in 1933–34 has continued, but has been delayed

through the necessity of securing collaboration of experts on various groups of animals. The description of the distribution of the population as a whole (total yield of vertical hauls) is complete, and is ready for publication as soon as the interpretation put upon the findings is checked by the hydrographic data and by the analysis of the behavior of individual species.

The Limacina collections have not only been counted but each individual has been measured, yielding a very interesting picture of the growth and spread of a population on drifting into a new habitat.

The Sagittae have been identified by Miss Alice Beale and their distribution examined. The results confirm the earlier findings of Bigelow and Huntsman and throw some additional light on the current system of the Gulf.

The Copepods are being sorted and identified by Dr. C. B. Wilson. The identification of the Euphausids is nearly complete.

Miss Lillick worked during the summer on the phytoplankton collections and completed the study of the very complete collections made in April and May, 1934. The results show a distinct relation between the distribution of species and the established drift of the water along the shore of the Gulf. They also indicate a large area of relatively stationary water offshore in the northwestern quarter of the Gulf.

I am also preparing for publication in collaboration with Homer P. Smith and Bostwick Ketchum a paper on the distribution of phosphorous compounds throughout the year at a standard station 50 miles northeast of Highland Light. By separating the phosphorus into its organic and inorganic fractions and into that part present in particulate matter, new light is thrown on details of the phosphorus cycle in a moderately deep body of water, where decomposition does not take place primarily upon the bottom. Owing to the seasonal fluctuation in the quantity of organic phosphorus in the water, deductions may be drawn concerning the intensity of decomposition at various depths, and of the extent of the eddy conductivity involved in restoring inorganic phosphate to the surface waters.

A paper is also in preparation containing the results of observations made by Dr. Ancel B. Keys and myself on the ammonium content of the waters of the Gulf of Maine.

Mr. Bostwick Ketchum has continued his studies on the assimilation of nitrogen and phosphorus by the diatom, *Nitzschia*, in media of various nitrate and phosphate content. His results indicate that the ratio in which nitrogen and phosphorus are absorbed is dependent in definite ways upon the relative availability of these elements.

Dr. Richard Gould has made a study of the behavior of phosphorous compounds in the decomposition of *Arbacia* eggs. His results indicate that the phosphorus liberated from this material passes rapidly to the inorganic form, leaving no relatively stable residues of organic phosphorus compounds such as appear to accumulate in sea water.

Mr. Sidney Hsiao has been conducting experiments upon the growth of fishes and their scales under controlled conditions in the laboratory. During the summer he worked with pollock and cunners but found great difficulty in keeping the fish alive long enough for the purpose.

Mr. Robert Stauffer has been making ecological studies of a lagoon community after the disappearance of *Zostera*. He has made quantitative studies to determine the effect of the removal of this dominant member of the biological community upon the general composition of the animal community. Simplification of the environment due to the loss of vegetation was shown to be accompanied by a decrease of one-third in the total number of species without the appearance of any new species.

An investigation of the gases and the gas exchange in the mud of a tidal flat was initiated to give an understanding of the characteristics of the sea bottom as an ecological environment. This involved studies of the tidal circulation of the ground water in the flat, of the oxygen and hydrogen sulfide contents of the ground water, the amount of organic matter in the mud, and the oxygen consumption of the organisms of the mud. The outstanding characteristics of the environment appear to be a severely limited circulation of oxygen with a consequent accumulation of hydrogen sulfide and a limitation of aerobic metabolism to a rate much below the maximum for the actual quantity of organisms present.

DYNAMIC OCEANOGRAPHY

C.-G. ROSSBY

During the past year Mr. Montgomery and Prof. Rossby continued their investigation of the interaction between air and water. Particular attention was given to the problem of momentum transfer at the sea surface. Evidence was accumulated to show that a laminar sub-boundary layer develops next to the sea surface. The total force between wind and water appears to be the sum of the true frictional stress transmitted through this layer and of the resultant of the

horizontal components of the normal pressures exerted on the corrugated ocean surface. During light wind conditions the true shearing stress dominates, but during strong winds or unsteady conditions normal pressures play the more important rôle. During steady state conditions the total wind force may be computed by regarding the sea surface as a rough boundary with a roughness parameter of about 0.6 cm.

Mr. Montgomery's measurements of the humidity distribution in various heights above the sea surface have been completed and confirm the existence of a laminar sub-boundary layer.

A preliminary report on the effect of large scale horizontal mixing on the dynamics of ocean currents was published and presented at the meeting of the International Geophysical Union in Edinburgh in September. This investigation was based on the assumption that a well-defined ocean current system such as the Gulf Stream in its essential features may be compared to a horizontal wake stream in which lateral mixing brings about a gradual diffusion of momentum to the surrounding water masses. Wake streams have been studied both experimentally and theoretically, particularly in Göttingen, but the results obtained are not directly applicable to the phenomena in the ocean since they do not take into account the effects of the earth's rotation and of the stratification of the water. Thus the preliminary report was restricted very largely to a discussion of the modifications resulting from these two factors. Qualitative results were obtained with respect to the exchange of water between the current and its environment and these results seem to agree with observations.

The final section of the report was devoted to an analysis of the mixing between the Gulf Stream and its surroundings with the aid of oxygen-salinity correlation curves.

The investigation is now being continued and extended to include also an experimental study of wake streams in rotating tanks.

STUDIES OF THE DISTRIBUTION OF OXYGEN AND PHOSPHATES IN THE OCEAN, AND OF SUBMARINE VERTICAL OSCILLATIONS IN THE OFFING OF WOODS HOLE

H. R. SEIWELL

1. An analytical investigation of oxygen and phosphorus distributions and their relationship to the temperature, salinity, and density in the North Atlantic has been under way with the object of

introducing additional identifying properties into physical oceanographic studies. The use of these two non-conservative properties of sea water not only serves as a check on circulation concepts based solely on temperature and salinity characteristics, but frequently furnishes information regarding the origin and movements of the deep water masses of the oceans when temperature and salinity information fails.

2. The question of the origin of the principal oxygen minimum has again been brought into prominence and promises to become a controversial point among physical oceanographers. Accordingly, a rigid analysis of the details of this layer has been undertaken in an attempt to ascertain the facts surrounding the minimum oxygen value and to offer suggestions as to its origin and maintenance. The problem involves the biological, physical-chemical and physical relationships within the zone of low oxygen concentration, and is being attacked by making a mathematical analysis of the existing oceanic data and combining the results with those of laboratory experiments (in which I have been assisted by Gladys Eddy Seiwell) on the free fall velocity and oxygen consumption of dead plankton organisms.

3. In connection with our physical oceanographical studies of the North Atlantic, and, in particular, investigations of the oxygen poor layer, the question of short period vertical oscillations of the water column appears to play a significant rôle. During August, 1936, a five day station was established about one hundred and sixty miles northwest of Bermuda for the purpose of observing the vertical oscillations occurring throughout the entire water column of slightly more than 5000 meters depth. As a result we obtained definite information that short period oscillations, with amplitudes of 15 to 25 meters, having periods of twelve and twenty-four lunar hours, exist. The data have been subjected to a theoretical treatment and the results applied to practical oceanography.

It is expected that the results of these investigations will be published in 1937.

PHYSICAL OCEANOGRAPHY OF THE GRAND BANKS REGION AND LABRADOR SEA

FLOYD M. SOULE

In collaboration with Edw. H. Smith and Olav Mosby, the report on the physical oceanography of Baffin Bay, Davis Strait and the Labrador Sea (based on the measurements made on the "Marion"

in 1928 and "General Greene" in 1931, 1933, and 1934) was completed. The months of April, May and the first part of June were spent on the oceanographic vessel of the International Ice Patrol, the U.S.C.G. Patrol Boat "General Greene," in the region of the Grand Banks, supplying dynamic topographic charts of the region to the Ice Patrol cutters "Pontchartrain" and "Champlain." During this period three current surveys of the critical area were made with reference to the 1000 decibar surface although the temperature and salinity measurements extended in many cases to 1400 meters where the depth of water permitted. In this work 187 oceanographic stations were occupied on an abbreviated post-season cruise consisting of two sections, one between South Wolf Island, Labrador, and Cape Farewell, Greenland, and the other from 60° 09′ N latitude, 51° 15′ W longitude, to the mouth of Arsuk Fiord, Greenland. The measurements on the post-season cruise took place June 20–26, all stations being occupied from the surface to as near bottom as was practicable.

On the post-season cruise 295 fathometer soundings were taken. These soundings have been corrected, tabulated and supplied to the U. S. Hydrographic Office and the International Hydrographic Bureau. An additional 775 soundings taken in the Grand Banks-Flemish Cap region in 1933, 1935 and 1936 have been corrected, tabulated and supplied to the same agencies. Also on the post-season cruise the glacier front in Arsuk Fiord was photographed as in 1928, 1931, and 1933. This year the various distances of retreat and advance were measured by means of numerous sextant angles taken from both ends of a 600-foot base line.

Progress has been made in the analysis of the data collected on the 1935 post-season cruise and of the variations in the volume of flow and average temperature of the Labrador Current at three sections along the eastern edge of the Grand Banks which have been repeatedly occupied during 1934, 1935 and 1936. The oceanographic section of U. S. Coast Guard Bulletin No. 26, dealing with the work of the 1936 season, has been prepared for publication.

INVESTIGATIONS ON MARINE FUNGI

F. K. SPARROW, JR.

During the summer of 1936 work was continued on the general problem of the distribution of fungi in the sea. An attempt was made to determine whether or not free-living fungi existed in the marine humus. Offshore stations were established which varied from

18–220 m. in depth. Bottom cores were collected under as sterile conditions as possible and tested for the presence of fungi by ordinary plating methods. Flasks of liquid nutrient media were also used but proved impractical. All tests were appropriately controlled. Water cultures containing cores of bottom mud and "baited" with several types of common marine animals were also tried. Direct observations by the attached slide method and a microscopic examination of the mud proved unsatisfactory.

It was found by the plate method—using a solid nutrient medium in sea-water—that certain types of free-living fungi could be recovered from all samples (55) taken from the surface layer of mud cores. The middle and bottom portions of these cores yielded a total of one and three colonies, respectively, and the controls two. No results were obtained from the water cultures either at room temperature (21–24° C.) or at 6° C. The fungi recovered belonged to genera commonly found in land soils or recovered in spore form from the air. Spores of certain of these fungi proved viable after a week in sterile sea water.

With the present data it can now be said with some certainty that fungus spores are present in viable form in the surface layer of the ocean floor in certain localities at depths up to 220 meters.

Further observations were made on parasitic marine Phycomycetes and several possibly new species of marine Ascomycetes were collected. Finally, preliminary experiments on the presence of saprophytic fungi in accumulations of phytoplankton disintegrating under running water gave positive results.

STUDIES IN SEDIMENTATION AND ON THE GEOLOGY OF THE CONTINENTAL SHELF

H. C. STETSON

Dredging was continued in 5 of the submarine canyons of Georges Bank. Two new formations of hard sandstone were found in place on their walls. One of these is upper Cretaceous, the other upper Eocene. A new Miocene formation consisting of compact silt was also found. The position of these formations checks with stratigraphic assumptions published on the dredging of 1934.

In October a series of cores were taken down the continental slope south of Martha's Vineyard from the 100 fathom curve, nearly to 2000. The trip was made to determine, by tracing seaward, whether or not a compact clay formation found in every valley is fill or part

of the actual wall. The new coring tube designed by C. S. Piggot was used. This tube, actuated by a cartridge containing high explosive, was able to penetrate the surface layers of sandy silt, which a weighted tube will not do, and in every case the clay was found lying beneath them. Evidently they are a veneer deposited in the canyons as well as on the continental slope.

Current measurements were taken in the bottoms of three of the canyons. An Ekman meter was suspended in a frame which was so constructed that the messengers, to start and stop the mechanism, were released when the legs touched the bottom and when they were lifted off. Readings were obtained within six inches of the bottom between 240 and 210 fathoms of water. The velocities never exceeded .01 knots. The currents are controlled by the tide-flow up the canyon on the flood and downwards on the ebb. This same instrument was used on an anchored station 23 miles south of Block Island.

The results of the 1934 canyon dredging have been published in full and a preliminary report published on the results of 1935. A paper on the sediments of the Ross Sea based on cores obtained from the second Byrd Antarctic Expedition has been completed.

A petrographic study is being made by W. F. Wrath of the samples obtained in various tows and cores from all the canyons as an aid to correlating the different formations. He also carried out some experiments on the compaction of sediments under the impact of the coring tube. The data were worked up and the results published.

NITROGEN CONTENT OF THE PARTICULATE MATTER IN THE SEA

TH. V. BRAND

The vertical distribution of the nitrogen contained in the particulate matter (nannoplankton+detritus) has been studied at one deep sea station of the Sargasso Sea, one station in the offshore waters and four stations in the Gulf of Maine. A paper on this subject has been prepared.

A search was made for fixatives suitable to the use of the carbon method. Satisfactory results were obtained with chromic acid (concentration in the water samples 0.5%) and potassium bichromate (concentration 5%). The method can now be used for surface samples. However, before it can be applied to samples taken with Nansen bottles, further tests are necessary.

STUDIES IN MARINE MICROBIOLOGY

SELMAN A. WAKSMAN, CHARLES E. RENN, CORNELIA L. CAREY,
MARGARET HOTCHKISS, MARGARET R. BUTLER,
ASSISTED BY J. L. STOKES

During 1936 the following problems in marine microbiology were investigated: (1) bacteriocidal properties of sea water, (2) decomposition of marine plankton and algal residues by bacteria, (3) rôle of bacteria in the decomposition of freshly synthesized diatom material, (4) bacterial transformation of nitrogen in the sea, (5) nitrate formation and reduction by marine bacteria, (6) occurrence and distribution of anaerobic nitrogen-fixing bacteria in the sea bottom, (7) the wasting disease of eel-grass, and (8) bacterial population of the deep sea.

An investigation of the factors relating to the low numbers of bacteria in natural sea water was made by S. A. Waksman and M. Hotchkiss. Fresh, unaltered sea water was found to have inhibitory and destructive effects upon pure cultures of marine bacteria introduced into it; these effects following an initial increase in numbers. Water sterilized by heat and Berkefeld filtration, and artificial salt solutions exerted no such destructive action. Seitz filtered sea water, on the other hand, was decidedly bacteriocidal—a property ascribed to the metals in the apparatus.

The decrease in numbers of bacteria in these experiments was not accompanied by a drop in oxygen consumption; suggesting that the animal population is very active both in the destruction of bacteria and in the oxidation of organic matter. This assumption can be used as a basis for explaining the low numbers of bacteria usually found in the sea.

The decomposition of marine plankton and of pure, persisting strains of diatoms by bacteria was studied by S. A. Waksman and M. R. Butler. It was found that marine plankton decomposes rapidly; the zoöplankton fraction being especially labile, and quickly liberating available nitrogen and phosphorus on bacterial decomposition. Diatom-rich plankton, however, decomposed more slowly; the nitrogen is freed gradually, while phosphorus is liberated more rapidly as phosphate. The bacteria do not show the expected increase in numbers during these processes, leading to the conclusion that animal forms and other organisms that do not show on agar counting plates must function in the processes.

In coöperation with the U. S. Biological Survey, C. E. Renn made a field survey of the Zostera beds in the shallow bays from Cape Cod south to Great Bay, New Jersey, studying the distribution of the

Labyrinthula parasite causing the disease, and incidence of wasting in newly developed beds. He also collaborated with Dr. Rakestraw and Dr. von Brand in a chemical study of the regeneration of nitrate from plankton. An apparatus was devised for taking uncontaminated specimens of sea water from unlimited depths and several stations were taken in the Sargasso Sea with very satisfactory results. The salt tolerance of several nitrogen fixing Clostridia from western soils was investigated as a preliminary to determining the probable function of these organisms in the sea bottom. Several phenomena previously reported and believed to limit bacterial activity in the sea itself were investigated.

Dr. C. L. Carey continued her studies on nitrification and denitrification in sea waters and muds. Nitrification has been previously demonstrated to take place in mud from near the shore, and some oxidation to nitrite has occurred in samples of mud from greater depths (5100 meters), but so far oxidation of nitrite to nitrate in such samples has not been experienced. Nitrate was formed in waters containing decomposing plankton where ammonia was being produced, and occasionally in sea water, but only where vertical mixing went on. An attempt was made to isolate the organisms causing nitrification in pure culture. Due to their slow rate of growth this project was not completed. Denitrification has been illustrated in Woods Hole water enriched with potassium nitrate and a suitable source of carbon, and also in mud samples from a depth of 5100 meters.

Dr. M. Hotchkiss continued her investigations on the occurrence and distribution of nitrogen-fixing bacteria in sea water and in the sea bottom. It was observed in 1932 that of these bacteria the anaerobic Clostrium was detected much more frequently than the aerobic Aztobacter, a relationship common to terrestrial soils. The Clostridium, producing carbon dioxide and butyric acid from fermentation of glucose, is more easily identified. Cultures of these organisms have fixed nitrogen, and the process is almost always associated with their presence in great numbers. During the summers of 1933, 1935, and 1936 some 70 samples have been tested; these included material from water, sand, algal material from near shore, diatom tows, water and bottom samples from stations visited by "Atlantis" in the Gulf of Maine and off Bermuda. Sand and algal material from near shore invariably contained the organisms; the bottom of Buzzards Bay and Vineyard Sound were well seeded with them, 10 mg. of the material giving the characteristic tests. They have also been detected in some stations in the Gulf of Maine more remote from shore, and in bottom material at 600 meters, but they have not been found in samples from the deeper stations at 1, 3, 4 and 5 thousand meters.

WATER MOVEMENTS IN THE GULF OF MAINE

E. E. WATSON

With the assistance of Mr. Arthur Cooper and Mr. Richard Hanau, the dynamic heights in the Gulf of Maine have been computed from the temperature and salinity survey carried out by "Atlantis" in 1933 and 1934. Charts of dynamic contours have been drawn for the surface, 40, 100 and 180 meter levels for September, October, March and May, and the April charts are now in preparation. Owing to its biological significance the 140 meter level has also been computed for the spring months. The general picture of a single major anticlockwise circulation at all depths, with its centre off the northern tip of Georges Bank, remains unchanged. The difficulty of fitting the dynamic heights at the various stations to produce a consistent contour map has served to emphasize the weakness of the theoretical assumptions on which the method of computation depends.

In collaboration with Henry Stetson, direct current measurements were made near bottom off Block Island and also in the deep western basin of the Gulf of Maine. The results show that currents as high as 10 cm./sec. occur at half a meter above bottom at 220 meters in the Gulf. Furthermore the current one meter higher is only slightly greater. As a knowledge of these boundary layer currents is essential, a meter more suitable than the Ekman is being designed to give rapid measurements.

LIGHT RECEPTION AND PRODUCTION IN DEEP-SEA ANIMALS

J. H. WELSH, F. A. CHACE, JR., R. F. NUNNEMACHER, AND T. H. WATERMAN

The closing nets, which had been in use on "Atlantis" during previous years, were modified by Dr. H. B. Bigelow and Mr. R. F. Nunnemacher, and operated very successfully during a deep-water cruise in September. Additional material from known depths was obtained for a continuation of the study of modification with depth in the eyes of crustaceans. (A paper on the eyes of the Acanthephyridae is in press.) Eyes of a number of cephalopods and fishes were also obtained and are being prepared for study.

A new portable cooling system enabled us to keep certain deep-water decapods living for the duration of the cruise. It also gave us a supply of cold seawater which made it possible to revive and keep living, for periods of several hours, some of the deep-sea fishes and

cephalopods which were being used by Mr. T. H. Waterman in a study of the physiological control of luminescence. Photophores were also sectioned by the freezing method and observations made on the color of the several component parts.

Diurnal vertical migrations, hence the probability of the perception of penetrating daylight, were found to be made by certain of the organisms livings at depths of 400 meters and greater. This fact was established by making hauls every three hours throughout the day and night.

STUDIES ON COPEPODS

C. B. WILSON

During the first half of the summer, an examination was made of copepod plankton collected in 1912, 1913, and 1914 by the "Grampus" and "Bache" of the U. S. Bureau of Fisheries. This material had been stored in the National Museum since it was first obtained and had never been examined. It was all sorted, identified, properly named and returned to the Museum in suitable condition for permanent preservation. There were about 500 vials.

During the last half of the summer a study was made of the copepod plankton gathered in 1933 and 1934 by the Oceanographic ketch "Atlantis" in the Gulf of Maine. Each catch was sorted into its separate species and their relative amounts recorded in order to obtain their quantitative distribution in the Gulf throughout the year. When combined with the localities at which each of the catches was made, this will give a more accurate knowledge of the movements of the plankton as a whole as well as of its component species. These movements can then be connected intelligently with the varying physical and chemical conditions of the different portions of the Gulf through the changing seasons. One hundred and twenty-five of the catches were finished and 75 are left for future examination.

SAMPLING RELIABILITY OF PLANKTON NETS

C. P. WINSOR AND L. A. WALFORD

Our study of the published data has led us to the conclusion that the variations encountered in plankton hauls can be analyzed into two essentially distinct portions; one arises from the local irregularities in distribution of the organisms, while the other arises from variations in the actual hauling of the net. These results have been published.

Our further experimental attack on the problem has been with the objects, first, of providing evidence as to the nature of the local distribution, about which we were obliged to make assumptions which, though appearing reasonable to us, were without direct support; and, second, of obtaining more definite and detailed information as to the variations arising through the technique of hauling and counting the sample.

For this purpose, various techniques of obtaining simultaneous hauls in the same locality were tried. It was found that nothing short of mechanically coupling the nets would suffice to eliminate considerable variations from one net to another. We made a considerable number of vertical hauls, using three nets mechanically coupled.

The work of counting the material is still in progress; but it is possible at present to say that everything points toward a complete justification for our assumption of an essentially random local distribution of plankton. Further, the indications are that we may be able to analyze to some extent the nature of hauling variations; and finally, that we may be able to set definite standards which can be used to determine the accuracy of plankton hauls, or which can be used in determining the hauling procedure necessary to obtain results of any desired standard of precision.

In addition to this material, Dr. George Clarke has kindly placed at our disposition the results of two series of successive oblique hauls made in rapid sequence in the same area. This should provide valuable information as to the total variation to be expected in successive hauls.

List of Contributions

LIST OF CONTRIBUTIONS

FROM THE WOODS HOLE OCEANOGRAPHIC INSTITUTION

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